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CONTENTS

THE PRAIRIE

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THE PRAIRIE

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Little bluestem (*Andropogon scoparius*) prairie in midsummer with a lower layer of *Antennaria campestris* and an upper one of *Petalostemon candidus*, *Amorpha canescens*, and *Liatris scar*[illegible]

CONTENTS

THE PRAIRIE*

INTRODUCTION

This research is the third of a series of investigations on the prairie. The first dealt with the environment of the prairie (Weaver and Himmel, 1931). The second was concerned with the ecology and relative importance of the dominant grasses (Weaver and Fitzpatrick, 1932). The present study treats of the structure of the vegetation in the several types of prairie, the secondary grasses, the ecology of the forbs, together with a general survey of contacts, invasion, and succession. These investigations have resulted from years of intimate association with the great grasslands of North America. They were made in an endeavor to clarify some of the many problems presented by this vast natural unit of vegetation, to better understand the importance and significance of grassland—and hence its utilization—and to furnish a permanent record of a rapidly vanishing vegetation. It deals with the vegetation as it exists today; nature's yearly productivity unmodified by the hand of man except as he harvests the crop of hay in autumn.

The prairie covers a vast area. It appears almost monotonous in the general uniformity of its plant cover. The absence of trees, the paucity of shrubs and half-shrubs, the dominance of grasses, and a characteristic xeric flora constitute its main features (Fig. 1). Neither geological formation, topography, nor soil determines the character of the flora which develops under the master hand of climate. In varying the water relations of soil and air they merely bring about changes in the groupings of the dominant grasses and accompanying segregations and rearrangements of the forbs. Over the hills of loess with their deep mellow soils, across the hills, ravines, and valleys of the areas of glacial drift, far out on the level loess plain, and extending across the well drained alluvial lowlands along the Missouri and Platte Rivers and a thousand tributaries, extends the carpet of the prairie. It is a sea of waving grasses dotted with splendid flowers which nod gently before the summer breeze (Fig. 2).

EXTENT AND LOCATION OF AREA

The area investigated in this study lies in six states. It includes the grasslands of the western one-third of Iowa and those of approximately the eastern one-third of Nebraska. On the south it extends into Missouri and Kansas to the Kansas River. Northward it includes a small portion of southwestern Minnesota and a larger one of southeastern South Dakota. The prairie grasses dominate this whole region and forest is represented only

* Contribution from the Department of Botany, University of Nebraska, no. 82.

FIG. 1. Upland prairie near Lincoln, Nebr., June 17. The most important grass is *Andropogon scoparius; Psoralea floribunda* is the conspicuous forb.

FIG. 2. Low prairie near Glenwood, Ia., Sept. 1. The general height of the grass is 2.5 feet, which is exceeded by the coarse *Silphium integrifolium*. Light colored plant in foreground (mowed) is *Artemisia gnaphalodes*. Postclimax woodland along a stream.

by narrow belts of postclimax woodland along the streams. In addition there is the greater forest area, sometimes 2 to 10 miles wide, along the Missouri River (Aikman, 1929). In this vast tract of over 60,000 square miles, 135 representative areas, each 20 to 360 acres in extent, were selected and carefully studied. They were chosen so as to represent typical topography and also to obtain, so far as possible, rather uniform distribution throughout the region (Fig. 3). The results here recorded are believed to apply, in the main, to a much larger area.

This area is bounded on the north by about latitude 43.5° and on the south by 39°. It extends approximately from 94.5° to 98° west longitude. Altitudinally it varies from about 700 feet along the Missouri River at the mouth of the Kansas River to slightly over 2,000 feet in South Dakota.

The topography includes the loess bluffs which border the Missouri River, especially on the east, almost throughout its course across the area. These steep, bluff-like hills are, however, only a few miles in lateral extent. The whole area, with few exceptions, is drained by the Missouri River and its tributaries. Practically all of the area has been glaciated; the northern portion much more recently than the remainder. This part contains much rather level land (South Dakota, Minnesota, and Northern Iowa) as do also the unglaciated loess plains on the western rim of the territory. Most of the area, as in southern Iowa, eastern Nebraska, Missouri, and Kansas, consists of rolling hills separated by well drained ravines and valleys. These stand in sharp contrast to the broad, level flood plains of the Missouri and Platte Rivers and their numerous tributaries (Figs. 4 and 5).

CLIMATE AND SOIL

This portion of the prairie grows under a climate characterized by moderately long, cold winters and a long growing season with hot summers.[1] The growing season in the mid-prairie region (Lincoln, Nebraska) includes 160 to 170 days without severe frost. Awakening of the plants of prairie begins usually late in March and continues until the middle of April. Some plants continue activity until late in October. The season without killing frost extends on an average from April 20 to October 10. During the summer the average day temperatures sometimes reach 90° F. At such times the maximum daily temperature reaches or even exceeds 100° F. Such high temperatures, however, seem detrimental to the prairie vegetation only because of the decreased humidity produced by them. If sufficient soil and air moisture occurs, high temperatures seem merely to accelerate development. Average day temperatures are normally between 75° and 85° F., which is 10° or more higher than those for the night. Soil temperatures, under the cover of grasses, show a daily variation of 15° to 18° F. at a depth of three inches,

[1] For a detailed analysis of environmental factors of the prairie over a period of 12 years see Weaver and Himmel, "The Environment of the Prairie."

FIG. 3. Outline map of portions of the 6 states where prairies (marked x) were studied. The subdivisions are counties and the circles indicate towns and cities. The broken line across the southeastern part indicates approximately the isohyet of 32 inches. The tortuous line from Minn. to Kans. separates the Prairyerths on the east from the Blackerths.

but only 1° to 3° at 12 inches depth. Temperatures of both air and soil during the growing season are well within the ranges critical for plants of the prairie and are probably of secondary importance. Minimum temperatures of 15° to 20° F. or more below zero occur at intervals during the cold season when vegetation is dormant. The soil in the prairie freezes rather regularly each winter, usually after the middle of November, to a depth varying from 6 to 24 inches.

The prairie is typically a land of sunshine. During March, April, and May there is approximately 60 per cent sunshine but June, July, and August have 72 per cent or more.

Wind movement is fairly constant and often high. It is an important factor in promoting water loss. Evaporation varies greatly from year to year. It rarely falls below an average weekly loss of 10 c.c. per day and is usually between 20 and 30 c.c.[2] During periods of drought it sometimes reaches 40 to 55 c.c. High evaporation is correlated with low humidity and both of these with low water content of soil.

The average day relative humidity varies between 50 and 80 per cent during years of greater rainfall but falls frequently to 40 to 50 per cent during drier years. The average night humidity is frequently about 20 per cent higher. Both show weekly ranges of 8 to 20 per cent. No consistent differences were found throughout the three summer months. Low humidity practically always occurs during periods of low water content of soil and usually also during periods of high temperature.

The precipitation varies considerably at different stations in the prairie. The mean annual precipitation in the South Dakota portion is about 25 inches; that in Missouri reaches about 36 inches. At Lincoln, Nebraska, the mean annual precipitation over a period of 50 years is 28 inches. Its distribution is of the Great Plains type, between 76 and 79 per cent occurring between April 1 and September 30. Fourteen inches fall during the three months of May, June, and July (Loveland, 1920). Such a seasonal distribution of moisture is very favorable to the growth of grasses. Most of the precipitation during the summer months occurs in storms accompanied by thunder and lightning. Often the rainfall is very heavy over a short period of time. More than half of the precipitation of May, June, and July is from rains of an inch or more in 24 hours. Not infrequently, however, storms occur with a rainfall of 2 to 3 inches. During very heavy rains (4 to 6 inches in 24 hours) which occur infrequently, the soil is unable to absorb all of the water as it falls and the run-off is high. From 60 to 65 per cent of the precipitation occurs at night during the growing season, thus reducing the amount of water lost by evaporation (Kincer, 1922).

Periods of drought are liable to occur at any time and especially after

[2] From data obtained in the prairie at Lincoln, Nebraska, over a period of 12 years. Livingston's white, cylindrical, porus cup atmometers were used in these measurements.

midsummer. During a period of 13 years, for example, drought periods of 15 days or more, when the rainfall on consecutive days did not exceed 0.20 inch, occurred every year. A rainfall of less than 0.20 inch is probably

FIG. 4. Loess hills at Allen, near Ponca, Nebr., covered with tall-grass prairie. The dominant grasses are *Stipa spartea*, *Andropogon scoparius*, and *A. furcatus*. Photo. June 7.

FIG. 5. Low prairie near Union, Nebr., dominated by *Andropogon furcatus*, showing an abundance of forbs. *Liatris pycnostachya* in foreground and *Silphium laciniatum* standing high above the grasses. Photo. Sept. 5.

entirely intercepted by the vegetation and the dry surface half-inch of soil in which no absorbing roots occur. This is especially so if it is scattered over a few hours or followed by bright sunshine and wind. Thus the rain has no effect upon available water content unless the surface soil is already wet. In years of ample rainfall there were only one or two such periods, but in dry years there were four to six. That they are rather regularly distributed throughout the growing season is shown by the fact that six occurred in April, nine in May, five in June, nine in July, seven in August, and eight in September. There are almost always very light, scattered showers during such times but they are of little or no significance except in temporarily lowering temperature and increasing humidity. Frequently these periods of drought last for a longer time than 15 days; 22 of the 44 (1916 to 1928, inclusive) continued 20 to 32 days.

The average snowfall is about 27 inches. "As a rule snow covers the ground but a few days at a time after each snowstorm and the ground is covered with snow less than half of the time even during the months of heaviest snowfall" (Loveland, 1920). Much of the snow is swept by high winds into depressions, and thus often contributes but little to the supply of moisture of the soil upon which it falls.

The soils of this vast area may best be understood when studied from a dynamic point of view. Soils undergo a process of development, the controlling factors being climate and vegetation. The features assumed by the soil in its development from infancy through youth, maturity, and old age vary with the environment. "Pedologists are now agreed that the basic characteristics of normal soils are not in accord with their parent materials but are largely determined by the climate and vegetation under which the soils evolve and by the land forms [such as flood plains, uplands, etc.] they occupy" (Wolfanger, 1930. Cf. Shantz and Marbut, 1923). All stable, mature soils of a given climatic region belong to a climatic soil type. They tend to show a sequence of similar horizontal layers, irrespective of the type of underlying rock, the latter causing only minor differences (Marbut, 1923). These horizontal layers constitute the soil profile which has a profound effect upon the water, air, and nutrient relations of the soil and, consequently, upon root development and plant growth (Shantz, 1923). Thus soils and vegetation develop in a manner somewhat parallel.

Since both climate and vegetation of the great area under study are rather uniform throughout, the major soil types also have certain definite characteristics. Hence, the various minor subdivisions or local soil types need not be dealt with as such. The ecological significance of various soil types is related to their ability to supply water and the necessary nutrients to the vegetation. The cover of grassland is fairly similar in species, structure, and manner of growth throughout the region. The various kinds of prairie

that do occur are clearly related to water content of soil, but only obscurely, if at all, to local soil types. The soils of the prairie region belong either to the Blackerths or Prairyerths (Wolfanger, 1930). These two great soil groups (which extend from northern Minnesota and North Dakota in wide parallel belts to Texas) have so much in common that for a long time even field investigators did not recognize significant differences. "Both have dark colored A horizons, yellowish or brownish B horizons (typically reddish towards the south), and well developed granular structures. Both are relatively non-acid, unleached, and have ample stores of organic matter and mineral plant foods." Both also agree in having great depths and (in the region under study) a constantly moist subsoil. "They have all the features which 'good' soils should have" (Wolfanger, 1930).

The dark color of the A horizon, which is usually about 18 inches deep in this area, is due to the decay of humus from untold generations of plants under the moderate rainfall of the region. The granular structure has resulted in part from the downward alluviation of a portion of the colloidal clay, since the rainfall is sufficient to wet deeply the soil and the surplus water is not transpired too rapidly by the vegetation. The forces of weathering, especially repeated freezing and thawing and alternate wetting and drying, together with the favorable effects of the root activities, particularly those of the grasses, even in the deeper soil, have all combined to produce this excellent granular structure.

The Blackerths are somewhat darker in color and have a more nearly perfect granulation than the Prairyerths. They also possess a higher content of soluble mineral matter. The chief difference, however, is one of lime content in the subsoil. Owing to greater precipitation in the Prairyerths, the latter are lower in lime but not essentially acid (Fig. 3). In the Blackerth belt, which lies to the west of the Prairyerths, the lower precipitation, accompanied by a less vigorous growth and consequently decreased transpiration by the cover of vegetation, resulted in the accumulation of a lime layer in the subsoil at a depth of 5 to 8 feet. Under the greater precipitation of the Prairyerths this layer was not formed. The precipitation is adequate in amount to maintain a predominantly downward movement of water extending to the water table.

These soils offer approximately every feature in general conceivably favorable to plant growth. Water penetrates them readily, they are well aerated, the precipitation is low and the soil solution is relatively concentrated. This very abundance of nutrients probably diminishes the amount of water that would otherwise be required to produce the same crop of natural vegetation. "The virgin soils are moderate to high in all essential soluble organic and inorganic substances except phosphorus, and the proportion of this mineral substance is higher than that which prevails in typical pedalfers," i.e., forested soils eastward (Wolfanger, 1930). Thus the

Prairyerths and Blackerths, owing to their granular structure, slight leaching, and almost negligible fertilizer requirements, have been and are being extensively broken for the production of crops. But the quantity of water demanded by the richness of the soil usually exceeds the supply and thus water becomes the great limiting factor to plant growth.

Water content of soil in the prairie has been studied extensively and throughout a long period of years (cf. Kiesselbach, *et al.*, 1929; Weaver and Himmel, 1931). The following data from a somewhat centrally located station (Lincoln) are indicative of conditions in general. Northward and westward the soils are usually drier; southeastward and eastward they are usually more moist. Water content in the surface 6 inches of upland soil varied widely and rapidly, often 10 per cent or more during a single week. It was reduced to less than 5 per cent one to four times during eleven of the twelve years. Only twice during this period was the water content reduced to the hygroscopic coefficient.

Available water content in the 6- to 12-inch soil layer exceeded 5 per cent three-fourths of the time, but fell to 2 or 3 per cent at seventeen different intervals. At no time was the water available for plant growth entirely exhausted.

In the second, third, and fourth foot the water content was less variable. In general, there was a gradual decrease in the supply with the advance of summer. This was frequently temporarily interrupted, especially in the second foot, by heavy rains. The available supply usually ranged between 5 and 15 per cent. The maximum was 21 per cent and a few times the minimum fell to 1 to 3 per cent.

On the lowland available water content was 3 to 10 per cent greater in the surface foot and often 5 to 11 per cent in excess of that of the upland in the deeper soil. Extended measurements and study have shown clearly that water content of soil and humidity of the air are the master factors of the environment of the prairie. They have shown also that the climax vegetation is remarkably well adapted to these water relations.

COMPLEXITY OF THE PRAIRIE

The prairie offers problems of great complexity. It presents many changes in both major and minor variations. Responses to major changes in habitat are more striking, since more pronounced, but of no greater interest than the more minute ones that recur again and again in response to slight differences in the factors. Moreover, as the seasons advance, the panorama of the landscape varies to an extent that is almost kaleidoscopic in character.

Major variations in the plant cover are determined in part by the amount of precipitation. They result also from differences in topography through their effect upon run-off and exposure and consequent water relations. On low ground, the depth of the water table is a determining factor. The his-

torical factor of the development of the vegetation and the segregation of the several dominant types, e.g., *Stipa spartea* occurring predominantly northward and *Panicum virgatum* more abundantly southward, does not lie within the province of this study (cf. Harvey, 1908; Clements, 1920; Gleason, 1923; Woodard, 1924). Major variations within the types or consociations and the extent of the area occupied by each type are determined by increasing or decreasing regional precipitation and the accompanying conditions of greater or less humidity and rate of evaporation as modified by wind and temperature. Local variations are brought about by the nature of the soil, chiefly its water-retaining capacity but to some degree by its fertility as well. Only rarely is the soil so shallow that the presence of underlying rock modifies the character of the plant cover.

Within the prairie cover one finds the conditions of life severe. Though the soil is rich and deep, water is frequently scarce and the plants sharing it are legion. Deficiency of water usually occurs when the air too is driest, the temperature high, and the prairie perhaps swept by desiccating winds. The grasses respond by increasing their osmotic pressure, folding or rolling their leaves, and in other ways (cf. Weaver and Fitzpatrick, 1932). The changes are most marked on upland where conditions are most severe. For example, osmotic pressures among lowland dominants ranged from about 7 atmospheres to approximately 15 A.; but those of upland had a much greater range. During early summer when conditions were less xeric a pressure of 7 to 9 A. was obtained, but under the stress of drought this increased to 20 to 25 A.

So numerous are the individuals that those of greater stature shade the shorter ones, often to the extent that seedlings and lower leaves die for lack of food. Through thousands of years there has resulted an adjustment of the species to the environment (Frontispiece). The plants, with few exceptions, are remarkably free from disease, regardless of the weather; they are little injured by high winds or extreme heat. They may be harmed by late freezing or infrequently stripped of their leaves and battered to the ground by hail, but rarely or never killed. Those that were unfitted have disappeared; those that remained have reacted to the factors of the environment so thoroughly that as species they successfully meet the most severe conditions.

The problem of an adequate water supply has been met by the development of deeply penetrating, usually widely branching, and thoroughly efficient root systems. The perennial life habit is exhibited by all of the dominant species as well as by practically all of those that are secondary and subdominant. Reproduction is largely vegetative. Although seedlings are found distributed widely, certain species meeting conditions favorable to germination and early growth almost every season, yet studies now being completed indicate that the survivors are extremely few (Blake, 1934). The underground plant parts are storehouses of food during the long period of winter dormancy and

account for the rapid growth of the plants following their early awakening in spring.

The roots do not all draw upon the same soil level for their supplies of water and nutrients. In fact the root habit is so fixed in this respect that the various species may be grouped according to the layer or layers of soil

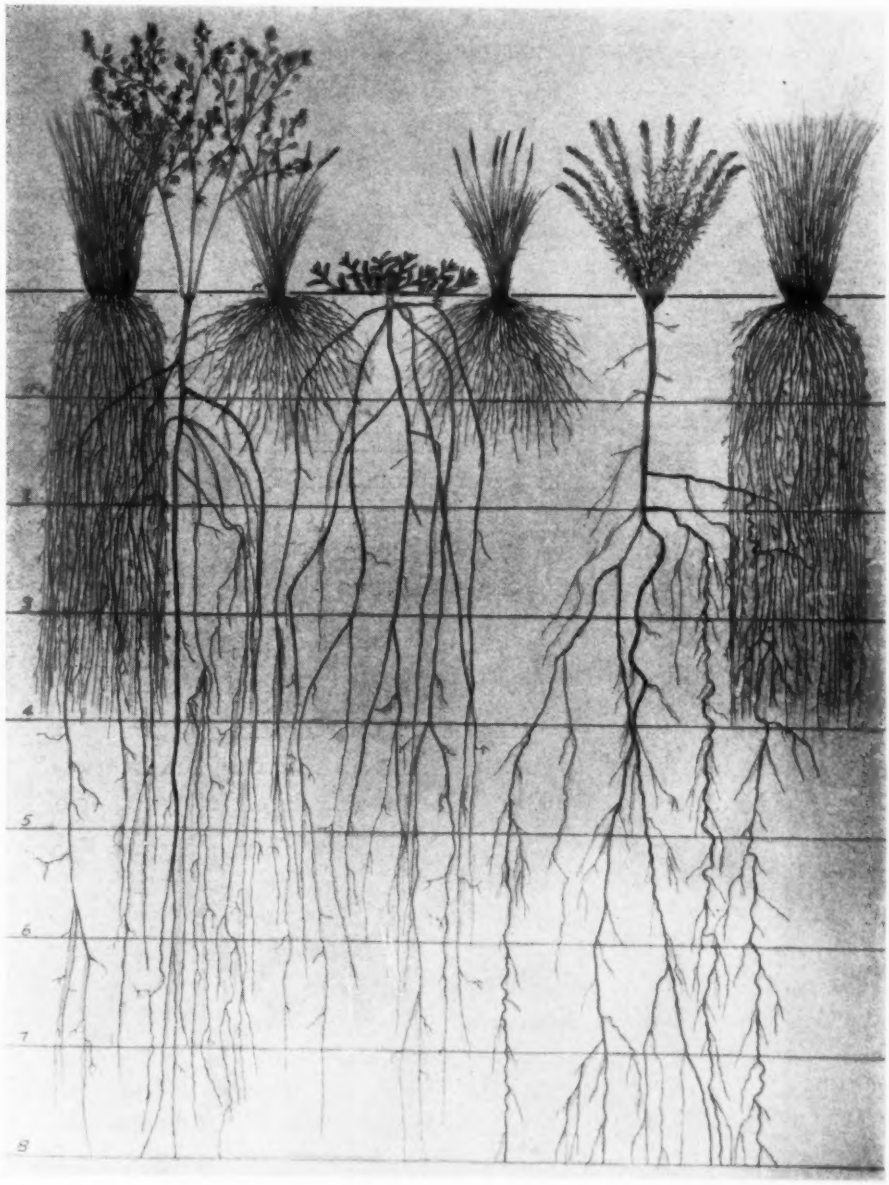

FIG. 6. Layers above and below ground: from left to right—*Andropogon scoparius, Psoralea floribunda, Koeleria cristata, Astragalus crassicarpus,* and *Kuhnia glutinosa.* Note the three layers below ground; that the grasses absorb at different levels; and that the forbs, which absorb but little in the first foot, extend much deeper, some to 17 feet.

occupied by them. Moreover, the species on a single square meter of soil surface frequently obtain their water and nutrients from a volume of 3 or more cubic meters of soil. For example, on upland prairie *Koeleria cristata* absorbs to a general level of about 1.5 feet; *Andropogon scoparius* extends its roots throughout the first 4 or 5 feet of soil. *Aster multiflorus* (*A. cricoides*) and *Amorpha canescens* (the latter enriching the soil with nitrogen throughout) penetrate to about 7 and 12-16 feet respectively. Indeed, the bulk of the prairie is below and not above the surface of the ground (Fig. 6). A similar layering of roots is also found on low ground (cf. Weaver, 1919, 1920).

This segregation of the root systems into several more or less distinct levels for absorption is one of the chief adaptations of plants of the prairie to their environment (cf. Woodhead, 1906; Sherff, 1912). Because of the extensive development of the absorbing organs, the soil is thoroughly occupied by the various root systems, especially the fine fibrous roots of the grasses, even to within one-half inch of the surface. The entire water supply is laid under tribute and competition beneath the surface is so severe during times of stress that the available water supply at all depths approaches but rarely reaches the point of complete exhaustion (Weaver and Himmel, 1931). The balance between species is so well adjusted that a considerable increase of one at the expense of another rarely occurs except in case of serious disturbance.

Just as roots occur at different levels, so too are found the underground parts primarily for food accumulation and propagation. Corms, bulbs, tubers, and root offshoots abound but much more frequently the rhizomes of grasses and forbs. These occur in dense masses, mostly within a very few inches of the soil surface or just below it. Roots and rhizomes form a dense network below the bunches and mats of sods. Between the plants or plant masses the water-absorbing system extends in so complete a network that invaders in the apparently bare areas can not successfully compete. The effect of this community habit and the excellent condition of tilth resulting from it is such that the soil rarely cracks with consequent exposure of large surfaces to evaporation as is frequently the case after the vegetation has been removed or seriously disturbed as in overgrazing.

Just what adjustments the species have made to live and successfully compete with their neighbors, to endure the conditions imposed upon them by the dominants, or to profit by the presence of their fellows are problems of great complexity but of extreme interest. The beauty and the quiet calm of the grassland should not obscure the fact that the prairie is a field of battle centuries old in which the conflicting species, never wholly victorious nor never entirely vanquished, each year renew the struggle. It is the bitter struggle for mere existence, for light, water, nutrients, etc., eagerly sought by numerous competitors. Each species would increase its holdings; but parent plants must compete with their own offspring; as a result the population becomes

enormously overcrowded for the best development of the individual. Consequently all are reduced in size and underdeveloped compared to the stature they could attain. They often fruit sparingly rather than abundantly, and take years to accomplish what, unhindered by their fellows, might be accomplished in a single season. Such is the picture of the prairie in its condition of stabilization (Fig. 7).

The plan of life in the prairie is very diverse. So many species can exist together only by sharing the soil at different levels, by obtaining light at different heights, by making maximum demands for the factors at different seasons of the year, by fitting into the niches unoccupied by other species, and by actually profiting by the incidental benefits afforded by the community of which they are a part. The legumes add nitrogen to the soil; the taller plants protect the lower ones from the heating and drying effects of full insolation; the mat formers and others prostrate on the soil further reduce water loss by covering its surface. They live in an atmosphere much better supplied with moisture than the windswept plants above. Light is absorbed at many levels, the more or less vertical leaves of the dominant grasses permitting some light to filter between them as the sun swings across the heavens.

Layering in the prairie is the result of a process of adaptation and selec-

FIG. 7. Layering in low prairie. Four layers are shown: 1, ground layer of *Fragaria virginiana, Viola papilionacea,* and *Galium tinctorium;* 2, *Steironema ciliatum;* 3, *Andropogon furcatus* and *Sorghastrum nutans,* two feet high, overtopped by; 4, *Elymus canadensis, Spartina michauxiana,* and *Asclepias sullivantii.* Photo. Greenwood, Nebr., Aug. 2.

FIG. 8. *Antennaria campestris* in July after the grasses have been removed. This species blossoms very early in spring.

tion that has taken place through past centuries. The more numerous the upper layers and the more completely they occupy the available space the greater must be the tolerance of progressively lower layers to reduced light intensity. Thus, in grassland as well as in forest, light is a factor of great significance. At a height of 12 inches it is frequently reduced to 25 to 35 per cent and near the surface of the soil often to only 3 to 8 per cent.

The prairie is a great stabilizer. Compared to man's crops of wheat or maize (in fields adjacent on virgin soil) fluctuations in temperature of both soil and air are much less in the prairie, humidity is consistently higher, and evaporation is decreased. The demands for water and light increase more gradually and are extended over a longer period of time. Less water is lost by run-off or by surface evaporation. When drought comes, the vegetation gradually adjusts itself to the time of stress. Growth decreases, less water is needed, many species do not bloom, and the landscape temporarily takes on a dry appearance, which is again replaced by the fresher one of green upon the advent of rain (cf. Flory, 1934).

The struggle for dominance between the two most important grasses furnishes a fine example of adjustment to environment. The sturdy big bluestem (*Andropogon furcatus*) with its great stature and ability to endure shading occupies the well drained alluvial soils and often moist lower slopes almost or quite to the exclusion of its smaller rival, the little bluestem (*A. scoparius*). But the latter, although only half its size, is a keen competitor in its way. Endowed with a finer and apparently more efficient root system and having only approximately half the transpiring surface of its rival, it holds the drier uplands and meets its antagonist on equal terms on midslopes or even on the lower slopes of xeroclines.

Spartina michauxiana, adapted to poorly aerated soils, needs not compete with the big bluestem. Indeed it has few efficient competitors. But between the well aerated, moist soil holdings of the big bluestem and those of Spartina, certain tall grasses, well adapted to the intermediate conditions, dominate.

Thus as one travels over the rolling hills and across the intervening valleys, the orderly sequence of the dominance of one species replaced by that of another recurs again and again, as often as the change in habitat warrants. For species of prairie are assorted in nature and grouped in a more or less definite manner. Each grouping denotes a particular type of habitat. Although some species are much less exacting than others and range widely, most associate with their particular fellows, at least in the main. Chance distribution plays some part, but it must be kept in mind that ecesis and not migration alone is the key to distribution (Clements, 1916).

Many forbs of early spring always remain near the surface of the soil. They make a rapid growth, flower, and produce seed early and thus complete the important work of the season before they are overshadowed by the

grasses. Such are the violets (*Viola pedatifida* and *V. papilionacea*), the ground plum (*Astragalus crassicarpus*), the wood sorrel (*Oxalis violacea*) and prairie cat's paw (*Antennaria campestris*) (Fig. 8). Throughout the summer such low growing species carry on their vegetative activity in the subdued light of the understory or later wither away. Certain species are probably too mesic to continue growth under the direct heat of the midsummer sun, and are actually benefited by the shade, the protection afforded from

FIG. 9. *Mesadenia tuberosa* in August, nearly 4 feet tall. In spring the leaves form a rosette near the soil surface.

FIG. 10. Young *Psoralea floribunda* 12-15 inches tall on June 1. Note extent of bare stems which are naturally spaced.

drying winds, and the community benefit of having the transpired moisture held about them.

Other species maintain their territory for a time by means of compact rosettes but later carry their leaves upward on the elongating stems to function on a level with the grasses or even above them. Such are the hawkweed (*Hieracium longipilum*), various species of Senecio, *Mesadenia tuberosa*, and others (Fig. 9).

Certain species, notably those of the genera Psoralea and Baptisia, but also including some species of Euphorbia, Asclepias, Apocynum, etc., for a long time avoid competition with the grasses by producing an elongated stem (sometimes 10 inches in height) before unfolding either their leaves or blossoms. The lower leaves, if any, are scale-like. An abundance of light is assured; the widely spaced stems scarcely interfere with the grasses; the crowns are spread at a level partly or entirely above them. After mid-

summer the stems may break near the ground line as a result of a natural process of abscission and the whole upper story of foliage cover furnished by them disappears before the wind (Figs. 10 and 11).

Still other species—and these are the real competitors of the grasses—demand leaf space from soil surface to leafy top, which often extends to a greater height than the grasses. Moreover, if clumps or bushes, the tops may spread and lean out over the grasses. *Solidago rigida*, *S. rigidiuscula*, *Liatris scariosa*, and *Silphium intergrifolium* are examples of the erect type; *Kuhnia glutinosa* and *Asclepias tuberosa* of the spreading one, which is also shown in an extreme case by *Ceanothus pubescens* (Fig. 12). But even among such species, often the leaves are loosely aggregated so that the light filters through (as in *Amorpha canescens*) while in practically all many of the leaves on the lower portion of the stems are lost by midsummer.

All gradations between the various types prevail. Thus by a differentiation of maximum activities of the various species (including dominant grasses) into four rather marked seasonal aspects and by photosynthetic work being done at various levels in the several layers, a denser population utilizes all the factors and is thus more secure from the intrusion of invaders. For although autumnal species start growth early in spring, their demands are relatively small at a time when those of early vernal and prevernal bloomers are great. The latter are entirely secondary in importance if indeed they have not disappeared before the autumnal bloomers have their turn. Between these two seasons estival species hold sway. In general, the forbs occupy the places between the grasses, only the most vigorous ones replacing them. The grasses likewise consist of those that are

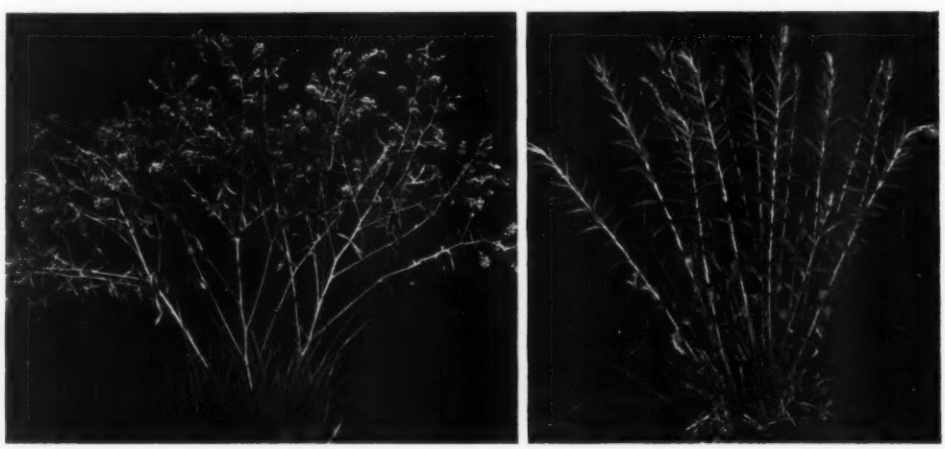

FIG. 11. *Psoralea floribunda* on June 20. Plant about 3.5 feet high and far overtopping the little bluestem.

FIG. 12. A small *Kuhnia glutinosa* in vegetative condition on July 12. This species is both abundant and widely distributed.

short, e.g., *Panicum scribnerianum, Bouteloua gracilis;* of midgrasses such as *Koeleria cristata* and *Andropogon scoparius;* and those of much greater stature such as *Sorghastrum nutans* and *Andropogon furcatus.* Where the latter are not too dense, the grasses also often form more or less distinct layers of vegetation.

In the uplands a ground layer of *Antennaria campestris* may be overtopped by one of *Panicum scribnerianum* and both by *Andropogon scoparius,* which in turn may form a distinct understory to *Psoralea floribunda, Euphorbia corollata,* and various other tall herbs.

Layering in lowlands is frequently even more pronounced, being due in part to the stature resulting from the more abundant water supply. An area of *Andropogon furcatus* and *Sorghastrum nutans* when two feet tall late in June may be distinctly outranked in height by relict *Elymus canadensis* and *Spartina michauxiana* which form a discontinuous layer 1 to 1.5 feet above them (Fig. 7). At the 18-inch level a distinct layer of *Steironema ciliatum* is common, and a lower one (at 8 to 14 inches) consisting of *Galium tinctorium, Oxalis stricta, Anemone canadensis,* and *Fragaria virginiana.* Moreover, in early spring the lower layer or layers alone may be represented. As the season advances there is a constant shifting and readjustment as the component species of higher layers continue to develop and increase their stature. As pointed out by Darwin, the greater the diversity of the structural units of a community, the better will all the space be utilized, and the greater will be the total plant population enabled to live in the given area.

OBJECTIVES AND PROCEDURE

The purpose of this study was to determine the nature, development, continuity, and intimate structure of a representative section of the most extensive and perhaps the most highly differentiated of plant climaxes, the Grassland Formation of North America. In traveling from one portion of a region to another, one notices variations in vegetation resulting not only from gradual climatic change but also from differences in edaphic and topographic factors. The study of a single area of grassland, therefore, no matter how complete, gives only a fragmentary picture of the prairie as a whole (cf. Thornber, 1901; Harvey, 1908; Steiger, 1930). The aim of the writers is to give a general view of the vegetation as a unit; to deal only with the more important facts, principles, and species and not to obscure these by unessential details.

This study is based upon the examination of 135 different tracts of prairie extending throughout the region. Many others were studied but they are not included because of some disturbance, small size, unusual topography, or more usually in order to maintain a more even distribution of the unit areas throughout the entire region.

Practically all of the prairies have been mowed annually, some for a period of more than fifty years (Fig. 13). It has been repeatedly demonstrated that removal of the plant cover after it is mature has no harmful effect upon the vegetation. Although the mowing is done close to the soil surface, there still remain 2.5 to 3 inches (often more on lowland) of unmowed stubble with dead basal leaves, among which accumulates fallen

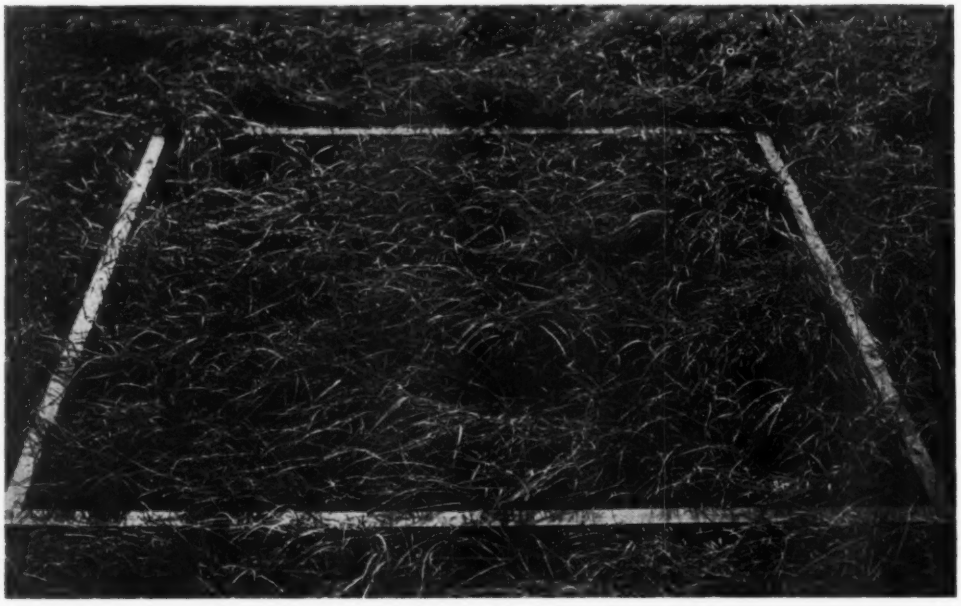

FIG. 13. Prairie after mowing and stacking the hay. Near Pierce, Nebr., Sept. 15.

FIG. 14. Detail of prairie late in March. The preceding fall was favorable to renewed growth after the upland prairie was cut for hay.

debris during "hay making", as well as the late autumnal growth. Consequently the soil is fairly well protected from erosion by wind and water, sudden fluctuations of temperature, and is by no means bare (Fig. 14). Occasionally mowing is replaced by burning or infrequently fire may run over the area in late winter or spring after the vegetation has been mowed.

Undoubtedly the removal of the plants does have an effect not only upon the quantity of organic material that would ultimately return to the soil but also upon the density and composition of the plant cover. Sampson (1921), working in Illinois, states: "Occasional local areas may be found that are seldom disturbed by man. It is in these least disturbed tracts where the dead grass remains from year to year that the dominant plants maintain their purest stand. The secondary species become insignificant, being represented only as scattered individuals here and there. . . ."

Experiments over a period of only 3 to 5 years have shown that the accumulation of debris greatly retards growth in spring. The soil warms more slowly since it does not receive the usual insolation. Not only is there an actual diminution of the basal cover, but also certain of the smaller and earlier species are greatly handicapped in growth and tend to disappear. Thus, occasional fires every two or three years renovate unmowed prairies and are distinctly beneficial if they occur in spring before growth is renewed.

Fires were undoubtedly frequent in prehistoric times—fires set by lightning or started by the Indians to clear the land and promote early grazing, make traveling easier, or for other reasons—while the enormous herds of buffaloes trampled down the grass, at least locally.

The prairies selected for study were of variable size. In several cases they were one-half to one square mile in extent. A large number consisted of one-fourth to one-eighth square mile, i.e., 160 to 80 acres. Some were 30 to 40 acres in extent and a few 20 acres, rarely less. The ease or difficulty of locating suitable tracts varied considerably. In certain portions of Kansas, Nebraska, and South Dakota they were still very abundant; in Minnesota and Missouri as well as certain sections of western Iowa they were rare. But where natural grassland does occur in highly cultivated sections, it usually is found in large units. Indeed, one of the major difficulties was the time and energy used in locating the fields to study. Some aid was obtained through a few county agents, but in the main the prairies were located only after local and repeated inquiry. More than 30,000 miles were traversed in making these studies. It is believed, however, that a sufficient number of prairies have been studied to permit reliable conclusions as to the composition or structure of the now highly fragmented grassland area (Fig. 15).

Two points of much importance should be emphasized. The remaining prairies are found on all types of topography and soils. Some occur on steep glaciated hills, others on hills of loess; considerable areas of broad "first"

and "second" bottom lands are still in grassland, as well as great areas of almost level uplands. Moreover, wherever the undisturbed prairie is found, it is unmodified by invaders from the surrounding cultural vegeta-

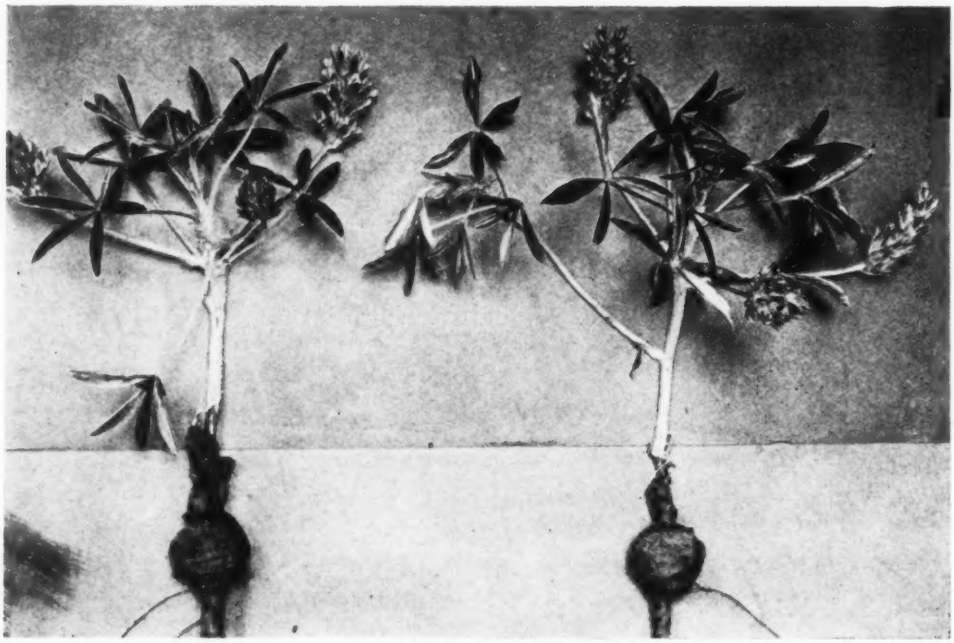

FIG. 15. High prairie near Corning, Ia., showing an abundance of *Ceanothus pubescens*.

FIG. 16. *Psoralea esculenta*, a perennial legume showing the swollen taproot where much food is stored. Plants about 6 inches tall, June 1.

tion. Sometimes tracts of grassland separated by many miles from their kind are entirely intact and, judging by other, continuous areas, quite unchanged. Just what changes have occurred from its condition 60 to 90 years ago when it formed a part of the magnificent prairie which seemed to continue indefinitely are unknown.

Methods of study combined both the extensive and intensive types. It should be pointed out that these studies were undertaken only after the writers, who have both spent many years in the grasslands, were very well acquainted with practically all of the species encountered. Preliminary studies were made so that the plants could be recognized in their vegetative stages of development. During later work, when any doubt existed, repeated and extensive collections were made and these were later compared with the same plants when in flower and fruit and with the numerous specimens of the local flora in the herbarium of the Department of Botany of the University of Nebraska. The latter had only recently been verified by the late Dr. P. A. Rydberg.

The investigators were left free, however, to give their major attention to the ecologic rather than the taxonomic phases of the problem. Moreover, the major emphasis was placed upon the more important species as regards structure and relatively little attention was given to the problems concerning distribution and variations of the rarer constituents of the flora. This circumstance was fortunate, because the ecological problems of the prairie alone offer a very complex field for study. In fact, over a considerable period of time, the endless variation in structure, the differences in distribution, and the changes wrought by the progress of the seasons, led to a feeling that each prairie was a study in itself and each one quite different from the others. But after continued investigation the whole problem was much simplified when it became clear that the grass patterns throughout the whole area (for the forbs are always of secondary importance) while indeed variable in detail, fell naturally into a few major and minor types.

Although many of the prairies were visited several times during the growing season, and perhaps half of them at least twice, yet some were studied at only one period. In fact, several fine tracts were found broken and others fenced and grazed when visited a second time, thus portending the final destruction of the native grasslands. Investigations were begun before the awakening of vegetation in spring and continued late into autumn. Frequent observations were also made during the period of winter dormancy. The actual quadrating and listing of forbs were done mainly between June 10 and August 10, mostly during a period of three years (1929-1931), a fourth summer being used as a check.

Owing to the abundance of food accumulated during the previous season, growth of the plants usually takes place with marked rapidity (Fig. 16). Even late blooming grasses practically complete their growth in height by

July 20, except in low wet soil; after this flower-stalk production occurs which makes them much more conspicuous (cf. Sarvis, 1923). Nearly all of the species of the autumnal aspect can be readily identified during this time if one has studied fully their vegetative parts and previously followed them through their annual cycle. Until well past midsummer, vernal species can still be easily found and recognized.

Only a few short lived plants may have escaped the searching scrutiny given to the different areas, and these, of course are at best of only minor ecological importance. It is not assumed, however, that some species may not have been overlooked in the study of any area, especially areas of larger size, for it is well known that only by frequently repeated visits can one be reasonably certain of no omissions. The writers feel confident, however, that all of the ecologically important plants have been listed and given their proper rank in every case. Moreover, the extended period of the study from year to year tended to check out seasonal variability in abundance or annuation.

The writers were nearly always accompanied by one or two graduate students who were of great assistance, especially in quadrating and in similar work. All work was done either by the former or in conjunction with the latter. The authors are especially indebted to Mr. Samuel B. Shively, who assisted continuously during two field seasons, and to several others who aided through shorter periods.

Upon entering a prairie, the first problem was to gain a preliminary knowledge of the type or types of grassland (consociations) it contained, their local extent and relative importance. This was accomplished by traversing the area on foot in at least two different directions. The types of vegetation were studied in detail and transitions from one to the other carefully noted. It early became apparent that the prairies could not be satisfactorily studied as one might study a forest from an airplane, however slowly propelled just above the crowns of the trees. Just as one arrives at the structure of woodland by working among the trees and undergrowth and studying the relationships of the groups and individuals, so also one to understand the plants of the prairie must get down to the ground and consider the individuals and their interrelationships in a similar manner. Where there is a broad shallow ravine, for example, observations of the tops of the grasses would indicate rising land. The grasses in the ravine may exceed in height those on the slopes by 50 to 100 per cent and thus much more than compensate the depression of soil surface due to the change in topography.

The surveys were not superficial, hundreds of yards were traversed on hands and knees, the surface of the plant cover was penetrated to determine of what it was constituted and how it was constructed—a most interesting and fascinating task. It was fortunate that the development, distribution, and interrelationships of the parts below ground were already well under-

stood in the case of most dominants and subdominants (Weaver, 1919, 1920; Clements and Weaver, 1924; Clements, Weaver, and Hanson, 1929).

Scores of quadrats and numerous transects were employed. Not only were the percentage composition and amount of basal or ground cover determined regularly in the different types, but also the manner and conditions under which one type gave way to another. The square meter quadrat was uniformly employed. The boundary of the area as well as its subdivisions into square decimeters was delimited by means of narrow strips of strap iron which were thrust through the grass on edge at the soil surface, and, once in position, fastened in place by appropriate steel pins. Each of the 100 square decimeter areas thus delimited was carefully scrutinized, divided into quarters, and the amount of plant cover at the surface of the soil, i.e., the basal cover, thus determined. This was at first a performance both slow and tedious. But with two men working on one quadrat and a third recording their results from each unit area, work was facilitated to such a degree that the basal cover of a score of quadrats could be determined in a single day.

Practice gave a high degree of accuracy, as was shown by comparing the areas determined from the same quadrats after actual mapping. For example, a rechecking of the same quadrat by a third investigator usually increased or decreased the percentage only 1 or 2 for the quadrat, an insignificant error considering the actual variation in the basal cover in adjacent unit areas.

The basal or ground cover, i.e., the actual area occupied by the stems, mats, or tufts of plants at the soil surface, is fairly stable and varies but comparatively little from year to year. The area occupied by species that grow in bunches or mats of sod (and this includes all of the dominant grasses) is rather accurately expressed in terms of basal cover (Sarvis, 1920). The foliage cover or the area occupied by the spreading tops of the plants in the several layers of vegetation above the surface is very changeable not only from one year to another but also with the development (and in some cases the natural disappearance) of the tops of the plants even from week to week. As pointed out by Cain (1932), in grazing work, for example, it was early discovered that a knowledge of the total spread of the foliage was practically useless information because of its great variability (Figs. 17 and 18). Consequently careful measurements were made of the basal cover because this could be done more accurately. Close estimates were regularly made, however, of the foliage cover, although the several layers were not considered separately. Where the vegetation was so dense that the tops of the plants entirely obscured the soil, the foliage cover was considered 100 per cent. Actually in some cases it would have totaled more if the percentage of cover of the several layers had been added. Where one-fourth of the soil was exposed when the tops of the plants were projected on the ground the cover was designated as 75 per cent. No cover

FIG. 17. New growth of bunches of *Andropogon scoparius* showing basal cover after burning. Mound City, Mo., May 7. The spreading tops soon develop a foliage cover of 75 to 90 per cent.

FIG. 18. Basal cover of *Andropogon furcatus* in practically pure stand on low ground, Union, Nebr. The plants were cut and photo. taken on June 24. The tops spread widely and the foliage cover was 100 per cent.

classes were used but the estimates were made to the nearest 5 per cent. Some quadrats for basal cover were made in September.

The percentage of the various species of grasses and sedges and the abundance of forbs were also determined in a total of more than 400 quadrats. In the early work this was done for each square decimeter, a time consuming procedure. The procedure was later modified so that a strip of 10 square decimeters was determined as a unit with equally accurate results. This led to the employment of a far larger number of quadrats than would have been possible otherwise and, hence it is believed, to a much more representative picture of the average composition of the plant cover.

Little attention was given to the infrequent and minor constituents among the grasses, none being recorded unless they constituted at least one-half of one per cent of the cover. The problem of forbs was greatly simplified since, in quadrating, the proper percentage of ground cover was allotted to them not as species but collectively. Since the forbs occur as individuals or individual groups their importance is best expressed in terms of size and abundance per unit area.

The basal cover controlled by different forbs is extremely variable. In the case of those with erect stems and few or no basal leaves, it is merely the cross-sectional area of the stems. Where the basal foliage is so thick as to be controlling, this too must be included. The cover of mat formers such as *Antennaria campestris* is equal to the actual spread of the leaves upon the soil. In *Astragalus crassicarpus* it corresponds to the parts of the branches that are held little or not at all above the soil surface and are in addition so closely crowded and densely clothed with leaves as to control an area several inches radially from the base (Fig. 19).

Sometimes the forbs are densely aggregated. In a single square meter of upland prairie, for example, which had a foliage cover of one-half grass and one-half forbs there were found 37 stems of *Solidago rigidiuscula*, 29 of *Amorpha canescens*, 43 of *Aster multiflorus*, and 2 seedlings of *Senecio plattensis*. Sometimes a single clump of *Silphium laciniatum* may occupy more than half of a square meter.

As a result of continued quadrating, one becomes enabled to judge accurately the composition of a small area of vegetation without delimiting it with quadrat straps. Thus the actual quadrats were repeatedly supplemented, especially during the last year of work, by careful estimates in many parts of an individual prairie. The detailed study thus imposed upon the investigators revealed much concerning the life histories, habits, and interrelationships of the various species that might easily have escaped attention if only general observations had been made. It also greatly decreased the probability of overlooking the relatively unimportant species or indeed the presence of inconspicuous ones.

In each prairie the relative abundance and importance of each species

Fig. 19. A single plant of *Astragalus crassicarpus* with a spread of top of about 2 feet, showing partly reclining branches, and fruits. The grasses have been removed. Freeman, S. Dak., June 8. (cf. Fig. 6).

Fig. 20. Portion of a society of *Anemone canadensis* in low prairie in June. This species usually occurs in dense stands.

other than the grasses were also studied and closely estimated. The various species were placed in one of each of five classes or ranks ranging from the chief society formers to plants of infrequent or rare occurrence. The relative ranking was determined only after carefully studying the abundance, size, duration, density, gregariousness, and basal and foliage cover of each species concerned. This demanded a rather detailed knowledge of about 75 species of upland prairie (others were of little importance or irregular in occurrence) and 67 from the lowland. Each offered more or less of an individual problem the solution of which was gained only after much field experience. The criterion in all cases was the actual effect of the forb upon the cover of grasses and the portion of the ground and foliage cover that it actually occupied. To ascertain these facts both minor and major quadrats supplemented extensive estimates and the development of each species was followed in detail as is shown in the study of their autecology. The estimates throughout the many square miles of prairie, preceded by careful studies in many areas, are believed to render more nearly correct the averages than would detailed counts in a few small sample plats even if worked out in far greater detail.

Forbs that occurred in great abundance and were of considerable importance in any particular prairie were given a ranking of 1, i.e., a society of the first class. These were widely, but not necessarily continuously distributed throughout the prairie. Where the plants were of large size and occupied considerable space more or less to the exclusion of the grasses, e.g., *Ceanothus pubescens*, *Silphium integrifolium*, and *Kuhnia glutinosa*, the species of considerable abundance were given this high ranking. On the other hand, such species as *Erigeron ramosus*, *Linum sulcatum*, and *Equisetum laevigatum*, which require relatively little space and are of smaller stature and especially very limited lateral spread, received a ranking of 1 only when they were extremely abundant, often 50 to 100 or more per square meter (Fig. 21).

Most of the important forbs fell between these extremes, that is they were of intermediate size and spread of tops so that these factors could be more easily correlated with the factor of abundance. A few mat-forming plants, such as *Antennaria campestris*, were important only in the ground cover; others like *Euphorbia corollata* were represented near the soil surface by a slender stem and branched widely only above the grass layer. Still others such as *Solidago glaberrima* and *S. rigida* were rather uniformly leafy from the base and thus had their effect below, in, and above the general foliage cover of the grasses (Fig. 21). Some species, such as *Anemone canadensis*, *Corcopsis palmata*, and *Pedicularis canadensis*, often occurred in rather dense local societies scattered here and there throughout the prairie (Fig. 20). Thus the ranking of the species into classes of relative importance is a process to which fixed measurements can not be accurately applied,

FIG. 21. A thick growth of *Equisetum laevigatum* nearly 3 feet high in *Andropogon furcatus* sod. Union, Nebr., June 24.

FIG. 22. The golden meadow-parsnip, *Zizia aurea*, common on low ground where its very tolerant lower leaves successfully compete with the tall grasses for light. The plant is 2.5 feet tall. Photo. June 4.

at least over so extensive an area. Nevertheless after becoming familiar with the species it is entirely possible to make a very useful classification which illustrates their relative importance.

That the grasses are the dominants of undisturbed grassland of this great area and the forbs secondary in importance was repeatedly shown. One of the most locally abundant forbs is *Psoralea floribunda*. In some prairies the bushy tops were so numerous above the cover of little bluestem that at a distance the latter was all but obscured. Studies in 25 square meters of such an area showed that the grasses had a ground cover of 13.5 per cent, while that of the forb, which was represented by stems alone, was only about 1/100 of 1 per cent. The dry weight of the forb was practically half that of the grass. Thus basal cover is no index of actual plant production. A single large rosin weed (*Silphium integrifolium*) might outweigh the amount of grass produced in several square meters. The foliage cover of the grasses in the quadrat of Psoralea was approximately 80 per cent, that of the forb layer about 66. Yet in spite of its abundance the shade cast by the very open crowns of this legume produced little harmful effect upon the grasses. In fact, in late July when the stems of the forb broke at the soil surface and the tops were blown away, the foliage cover of the grasses appeared quite as dense as in other similar areas where no Psoralea had grown. Perhaps the grasses were actually benefited more by the nitrogen produced by the growth of this legume than harmed by its presence. While other forbs materially diminish the stand of the grasses, it is indeed rare to find any

considerable area, even locally, in undisturbed prairie where the importance of the grasses is exceeded by that of the forbs.

Forbs of great abundance and much importance but not sufficiently so to be ranked as a society of the first class were listed in a second grouping. On the other extreme, plants that were very widely scattered and so rare that they were found in only one or a few places were given a ranking of five for that particular prairie. Where they were of somewhat more frequent occurrence and importance the ranking was raised to four. A large number of forbs that were not sufficiently important to be given second rank were found in almost every prairie, but were of too great abundance and occupied so much space in the plant cover that they were assigned to an intermediate ranking of three. Thus while the ranking of any particular species varied from prairie to prairie, such a census of the population revealed the species which were of greatest importance in most of the prairies over the area as a whole; which were only locally so; and which were consistently present but in small numbers. It satisfactorily solved the problem of the presence or constancy of a species, i.e., its more or less persistent occurrence in all of the representative areas or "stands" of a certain plant community. Also, much light was thrown upon fidelity of the species, i.e., whether it was more or less definitely limited to a certain plant community or ubiquitous in its habit.

The names of all plants were listed when the plants were first observed but these groupings were made tentatively for each prairie only after the survey was well under way. When it was completed the rankings were changed or verified as further study warranted. After a number of prairies had thus been listed it was usual for independent investigators to assign the same relative ranking to a species in any particular prairie. Where any disagreement arose it was settled only after further study.

A record of the vegetation was also made by means of photographs. To realize fully the difficulties of photographing grassland communities and forbs growing among the grasses one must have had first hand experience. Three factors must be constantly taken into account: wind, sunshine, and lack of definition of the grass or forb half hidden and obscured by its numerous associates. A breeze sufficient to keep the vegetation swaying gently nearly always occurs and many of the days are windy. Bright sunshine is the rule and with it one can not depict depth in the vegetation or show the detail of slender leaves or flower stalks against a background of cloudless sky. Only rarely are there times, especially following rainy weather, when diffuse light accompanies perfect calm. Even then so greatly detailed and complex is the vegetation that to portray properly individuality, a plant usually needs to be separated from its fellows. Many pictures were taken in the field, often with a curtained background, to present these complex relationships. But numerous plants were uprooted, usually with a

block of the native grasses in which they grew, removed to the laboratory where light and wind could be controlled and a "portrait" made to show the individual in detail with reference to the dominant grass. Some species are best understood when seen in their entirety. Special precautions were always necessary to maintain the plants unwilted. Much time and energy were consumed in this phase of the work. In every case great care was taken to obtain material representative as to size, branching, flowering habit, etc. (Fig. 22).

To summarize, the investigations in any prairie dealt with its type or types (consociations) of grassland, their transitions from one to the other, the basal cover, percentage composition in terms of the dominant grasses, and structure of the foliage cover. It also included a study of the forbs, their size, abundance, duration, and importance in the plant cover. The problem comprehended an ecological analysis of the vegetation so that it might be understood and studied as an organic unit.

TYPES OF GRASSLAND

The vegetation of the climax prairie consists of several major and minor consociations or types. In addition there are the later stages (associes) of the hydrosere, consisting of sedges, rushes, and hydric grasses leading up to the prairie proper. Nearly all of these types occur throughout the great area wherever conditions of soil moisture are favorable to their development and they are ecologically related one to the other in a very definite manner.

BIG BLUESTEM TYPE
(Andropogon furcatus Consociation)

The two types of greatest importance and widest extent are those characterized by big bluestem and little bluestem respectively. The former is found on lowlands, the latter on upland soils (Figs. 28 and 36). *Andropogon furcatus* Muhl. is the most important dominant of the grasslands which occupy the broad lowland valleys of the larger streams in the true prairie association. According to Clements (1920), this is a part of the extensive subclimax prairie found to the eastward within the climatic region of the deciduous forest and represents its persistence in areas where the water content of the soil is high. This type of prairie extends far southward (Tharp, 1926; Schaffner, 1926; Bruner, 1931) and especially eastward beyond the area studied. Sampson (1921) states that *A. furcatus* was the dominant of upland prairies over the whole state of Illinois, little bluestem being dominant only on the lighter types of well drained upland soils. Similar conditions prevailed in eastern Iowa, parts of Missouri and elsewhere (Vestal, 1914; Shimek, 1925). The big bluestem type is nearly always dominated by a single species, *A. furcatus*, one of the two most important dominants of prairie. The autecology and importance of the ten principal native grasses

of prairie have been given so recently that a brief statement must suffice (Weaver and Fitzpatrick, 1932).

This grassland type is best developed on lower moist slopes and well aerated lowlands and is in practically complete possession of them. Sometimes it also occurs over limited areas on well watered, nearly level uplands. On lower and midslopes big bluestem not only shares dominance with little bluestem but also regularly forms 5 to 25 per cent of the grass cover in the

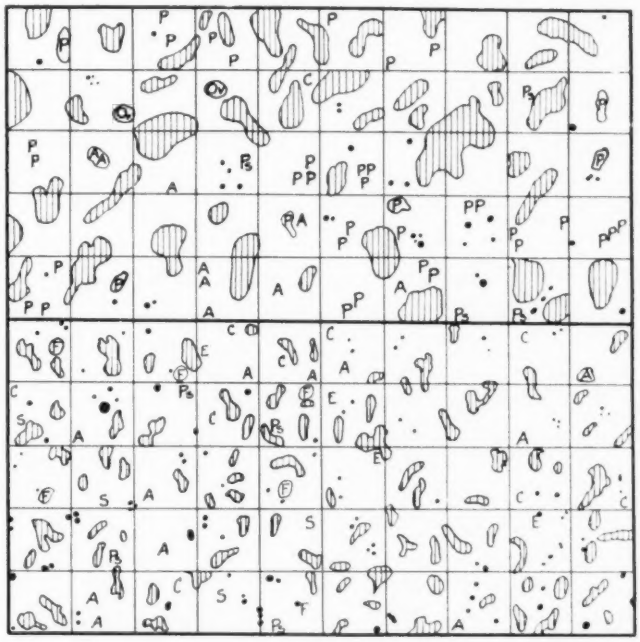

FIG. 23. Meter quadrat in *Andropogon furcatus* type: lower half in well developed lowland sod (as shown in Fig. 24); upper half illustrates bunch type found in drier areas. Vertical hatch or black dots, *A. furcatus;* P, *Poa pratensis;* Ps, *Panicum scribnerianum;* C, *Carex festucacea;* A, *Anemone canadensis;* E, *Equisetum laevigatum;* F, *Fragaria virginiana;* S, *Steironema ciliatum;* and Ov, *Oxalis violacea.*

Andropogon scoparius type of upland except on the driest hilltops and ridges. Thus its contact on the xeric side is usually with the little bluestem type. It is overwhelmingly exceeded in extent by the latter type over the area as a whole, but the two types together constitute fully 80 per cent of the grassland cover investigated.

The causes of dominance of big bluestem are found in its rapid development, dense, sod-forming habit of growth, great stature, and the tolerance of its seedlings to shade. Tillering begins early and is pronounced. The individual stems in well established sod are usually spaced more than a centimeter apart. They are grouped into mats of open sod with so much space intervening that the total ground cover in this type averages only about 13 per cent (Fig. 23). Nevertheless the foliage is so dense and spreads so

widely that the light is much reduced and invasion by other species is very difficult; it is indeed a closed community. The foliage cover varies in height from 1.5 to over 3 feet but mature flower stalks in late summer reach 5 to 10 feet (Fig. 24).

The big bluestem type of grassland yields 400-725 grams of dry matter per square meter by midsummer in the portion of the area with about 28 inches of precipitation. When the flower stalks have developed the yield under a precipitation of about 30 inches may exceed 1,000 grams.

FIG. 24. View in *Andropogon furcatus* consociation near Union, Nebr., on Sept. 1. *Artemisia gnaphalodes* prominent in foreground (cf. Fig. 18).

Big bluestem does not thrive in soil that is frequently saturated, and under such conditions it gives way to tall marsh grass, everywhere locally known as slough grass (*Spartina michauxiana*) or an intermediate type of grassland dominated by *Panicum virgatum* and *Elymus canadensis*.

Indian grass (*Sorghastrum nutans* (L.) Nash) is of southern derivation and reaches its greatest abundance in the southern portion of the area. Here it forms an important element in the big bluestem type. It may compose 90 per cent of the vegetation where almost pure areas occur in ravines, etc., but the percentage decreases to only 5 to 20 where it is ordinarily found abundantly in lowland mixtures. The more usual percentages over the area as a whole are 1 to 5 and in many lowlands, especially northward, it is almost absent. Where portions of the big bluestem type are occasionally flooded or otherwise disturbed Sorghastrum greatly increases in abundance. This tall, coarse, deeply rooted grass is very similar to big bluestem in stature, time of renewal of growth and flower-stalk production, and in its demands for a deep, moist, well-aerated soil. It often forms clumps of pure sod a few inches to a few feet in diameter, the coarse stems varying from 4 to 15 per sq. dm. Its occurrence in dense, big bluestem sod as isolated stems or very small clumps is more usual and results from the fact that under severe competition it tillers, if at all, only poorly.

Another grass of wide and variable distribution is probably found most

FIG. 25. Detail of *Spartina michauxiana*; general level of foliage 5.5 feet, the old flower stalks of the previous season are 7 to 7.5 feet tall. Photo, June 24.

FIG. 26. Detail of *Panicum virgatum* 3.5 feet tall on June 24. The old flower stalks of the previous season are 5 to 5.5 feet high.

abundantly in this type of grassland, although it also ranges widely over uplands. This is slender grama (*Bouteloua curtipendula* (Michx.) Torr.). It is a tall grass which reaches a height of 2 to 3.5 feet. Tillers arise abundantly from the numerous short rhizomes and the spreading base of the plant is well clothed with rather short leaves. Like most prairie dominants, it flowers mostly in August and September. It rarely occurs in great abundance, the largest undisturbed areas of which it has control seldom exceeding a few square meters. It nearly always occurs as small, isolated, rather open tufts scattered among the other grasses. A 1 to 3 per cent mixture is common but it may occur locally as abundantly as 10 per cent. This species increases markedly under grazing. Its tall stature and excellent absorbing system, together with its tolerance of shade, enable this grass to compete more or less successfully for a place in the sod.

The big bluestem type is clearly defined. Almost pure stands occur over extensive areas, except for a small admixture of *Sorghastrum nutans* and much less of *Bouteloua curtipendula*. *Poa pratensis* is of rather regular occurrence in the understory, as are also various species of forbs.

Slough Grass Type
(Spartina michauxiana Consocies)

A second type of grassland in soils too wet and consequently too poorly aerated for big bluestem, or even grasses somewhat more tolerant to these conditions, is characterized by slough grass. *Spartina michauxiana* Hitchc. is found in almost pure stands over vast areas of "first bottoms" along the Missouri River and to a smaller extent in similar situations along the flood plains of its many tributaries (Fig. 25). Such areas are really not a part of the climax prairie but the final consocies of the hydrosere leading to the prairie proper. Soils covered with this type of grassland are too wet for cultivation until they are drained. On its hydric side Spartina is preceded by various tall sedges, rushes, etc., such as *Carex vulpinoidea*, *C. hystricina*, and *Scirpus atrovirens*, which mark the transition to the reed-swamp stage. Toward the mesic side it gives way to a lowland type of grassland that is intermediate in its water relations between slough grass and big bluestem.

Spartina plays the rôle of a dominant because of its tall growth in dense pure stands. In fact it is taller than any of the other dominants of the lowlands, and where it shares marginal areas or occurs as a relict among other grasses it always overtops them (Fig. 27). Growth is more rapid than among the other prairie grasses. The general level of the foliage ranges from 3 to 7 feet depending upon the water supply, and the flower stalks in late summer are 5 to 6 feet tall in moist soil and 9 to 10 in wet areas. Because of its rhizome habit, it forms a dense sod. Where best developed the coarse, woody stems are widely spaced so that the soil surface actually occupied is often only 1 to 3 per cent (Fig. 29). Notwithstanding the usual

wide spacing, the shade is dense and where an abundant and constant water supply favors the growth of Spartina, other grasses are effectually excluded. This type is also frequent as ribbon-like belts in wet ravines, but slough grass rarely occurs in moist soils except in dry seasons or as a relict in soils that

FIG. 27. Relict *Spartina michauxiana* in *Andropogon furcatus* sod resulting from drainage. Hamburg, Ia., May 7.

FIG. 28. A fine stand of *Andropogon furcatus* about 40 inches tall, beginning to produce flower stalks. Glenwood, Ia., July 28.

have been drained. Many coarse forbs from both wetter and drier lowland types are found here, as well as numerous smaller ones in the understory.

Tall Panic Grass—Wild Rye Type
(Panicum-Elymus Associes)

An intermediate lowland type of much less extent and purity than either of the preceding is dominated by tall panic grass (*Panicum virgatum* L.) and nodding wild rye (*Elymus canadensis* L.). It occurs on soils where conditions are intermediate between those of the slough grass and big bluestem. Where the land slopes very gradually, broad areas are occupied by this type; but where the changes are more abrupt the two preceding types are usually separated by only a narrow belt of Panicum and Elymus. Moreover, extensive mixtures naturally occur on both margins.

Tall panic grass is a coarse, rank, sod-forming species (Fig. 26). It is more important in the southern and eastern portions of the area where the climate is more humid as well as warmer. Northward it is replaced to a large extent by nodding wild rye. It is rarely found in extensive pure stands, the clumps and areas usually alternating with Spartina, *Carex vulpinoidea*, etc. (Fig. 30). In such mixtures it constitutes 10 to 30 per cent or more of the vegetation over many square miles of poorly drained bottom lands. It is also found in areas of high water content along draws and the broad sloping flats receiving run-off water at the heads of draws. The pure, rank growth at the bottom of ravines where it is often 5 feet high, gradually decreases to about 3 feet near the top where the sod also becomes broken as the grass extends its area into drier lands. This grass is less tolerant of shade than is big bluestem; and it does not tiller so readily nor as abundantly; but during the first half of the summer it is distinctly taller. Where it has an abundant water supply, mature plants reach heights of 4.5 to 6 feet. Owing to the lack of basal shoots and the wide spacing between the unbranched stems, only a small amount (2 to 5 per cent) of the surface soil is actually occupied. In good stands only 4 to 24 stems occur per square decimeter and 95 per cent or more of the ground is bare (Fig. 29). Other species, especially *Poa pratensis*, may occur as an undergrowth but usually sparingly because of the low light intensity.

The codominant, *Elymus canadensis*, is also a tall, coarse grass very similar in its demands to the preceding. Hence it not only shares favorable areas but also, like the preceding, intermingles in transitional ones with Spartina on the one hand and *Andropogon furcatus* on the other. It forms pure stands only in very local areas. Elsewhere it usually constitutes a 1 to 5 per cent mixture among the other grasses, exceptionally 10 to 15 (Fig. 31). Northward and westward it becomes more abundant than in the south and east. Here on level lands subject to overflow it often covers large tracts, resembling thinly planted fields of barley. The actual part of the ground

cover formed by this species is small, usually only 5 to 8 per cent, since during midsummer there are few or no basal shoots or leaves. The rather woody stems occur in loose clumps or are widely spaced in a more or less continuous, open sod.

It does not compete very successfully with the other lowland grasses unless conditions are unfavorable to their best development. Elymus overcomes this handicap in part by its much earlier growth, which begins usually

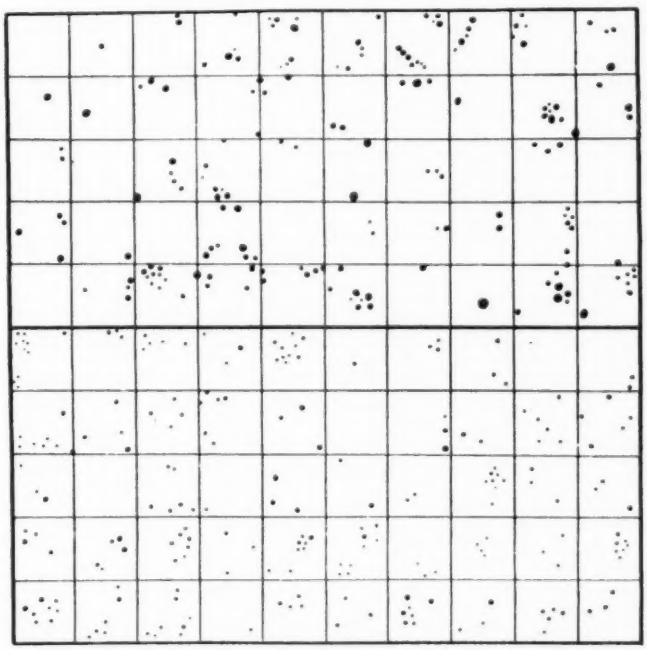

FIG. 29. Meter quadrat, upper half of *Spartina michauxiana* shown in Fig. 25. The black dots represent the stems of Spartina. Also one-half square meter (lower half) of *Panicum virgatum* shown in Fig 26. Stems of Panicum are indicated by black dots. A few of the following species occurred as a sparse understory to these grasses: *Carex vulpinoidea, Equisetum laevigatum, E. arvense, Aster salicifolius, Viola papilionacea,* and *Vicia americana.*

several weeks before that of its competitors. This gives it a distinct advantage in the struggle for light. It also flowers earlier. By the middle of June it reaches a height of 2.5 to 3.5 feet, the spikes appearing soon afterwards. These, with the elongating stem, add about another foot to its stature.

The forbs of this transitional type are naturally similar to those of both the more mesic and more hydric types with which it forms extensive contacts.

LITTLE BLUESTEM TYPE
(Andropogon scoparius Consociation)

Andropogon scoparius Michx. is the principal dominant of the most important upland type (Fig. 36). The little bluestem type is not only by far

the most extensive of those of uplands but it also occupies a portion of the area as a whole many times as great as that dominated by *Andropogon furcatus*. Like the big bluestem its dominance extends far beyond the confines of the area studied. It ranges somewhat over the uplands eastward, but especially southward, while westward it extends far into the mixed prairie

FIG. 30. General view of *Panicum virgatum* type with a few relict stalks of *Spartina michauxiana*, and *Andropogon furcatus* consociation in the background Photo. Sept. 6.

FIG. 31. General view of *Elymus canadensis* type.

(Shimek, 1915; Shantz, 1911). Little bluestem easily exceeds in importance all other upland species combined. It ordinarily forms an interrupted sod, the mats or tufts being so dense that few other species can invade. Accompanying species grow between the mats. On steep slopes where run-off and consequent erosion are great, the sod-mat type is replaced by a pronounced development of bunches. On the steep loess hills in the drier parts

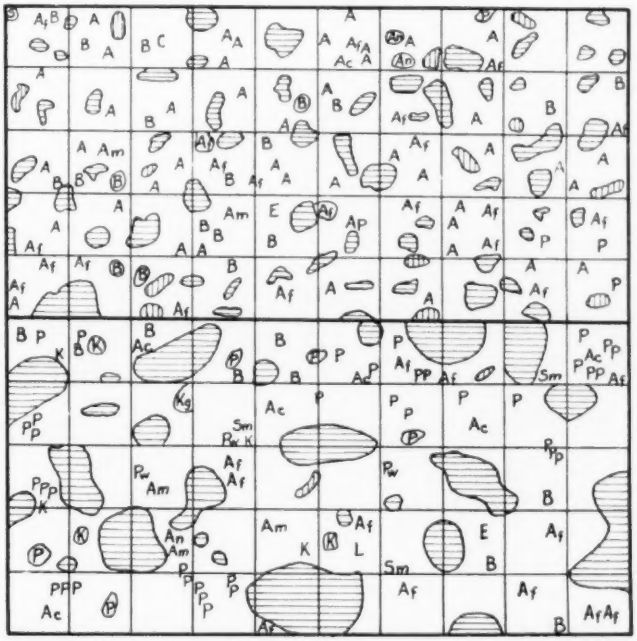

FIG. 32. Meter quadrat in *Andropogon scoparius* consociation: lower half in bunch type, upper half in sod-mat type. A or horizontal hatch, *A. scoparius;* Af or vertical hatch, *A. furcatus;* K, *Koeleria cristata;* Pw, *Panicum wilcoxianum;* S, *Sorghastrum nutans;* P, *Poa pratensis;* B, *Bouteloua curtipendula;* Ac, *Amorpha canescens;* C, *Carex pennsylvanica;* An, *Antennaria campestris;* Am, *Aster multiflorus;* E, *Erigeron ramosus;* Kg, *Kuhnia glutinosa;* and L, *Liatris punctata.*

of the area, little bluestem alone frequently constitutes 90 per cent of the cover of vegetation. In the north and northwest, especially on poor soils and areas with extreme run-off, it intermingles with needle grass (*Stipa spartea*) and in many locations is almost replaced by it. Southeastward, where moisture is more plentiful, its chief competitor is big bluestem, which intermingles profusely with it throughout and sometimes exceeds it in abundance, especially on the deep soil of loess hills. On midslopes and lower hillsides this type meets that of the big bluestem to which it almost uniformly gives way on the moist lower ground. But in drier soil over the area as a whole, including level uplands, *Andropogon scoparius* forms 50 to 60 per cent or even more of the vegetation.

Among the characteristics that make little bluestem such a successful

dominant are its vigorous seedlings that tiller both early and abundantly thus resulting in a compact, dense cover of grass. A fine, extremely well branched root system fills the soil not only beneath the mat but also on all sides of it, occupying the soil between the clumps. From 50 to over 300 leafy stems occur per square decimeter, the density of the bunch varying with water content of soil and with age. The size of the sod mats is variable. Usually they are 6 to 10 inches or less in diameter, and irregular in shape. Often the sod consists of smaller tufts closely aggregated so that the overlapping leaves constitute a foliage cover of 80 to 100 per cent. The ground cover in any case seldom exceeds 25 per cent (Fig. 32). The rather narrow and relatively short leaves form a foliage cover that varies in height in late summer from 7 to 12 inches on dry uplands, but increases to 15 inches or more in more favorable situations.

Flower stalks are produced in abundance only in wet years or in more favorable situations. Then they are abundant during late summer and autumn, reaching a height varying from 1.5 to about 3.5 feet. The little bluestem type of grassland yields 350 to 500 grams of dry matter per square meter by August and somewhat more in years of unusually favorable rainfall after the flower stalks have developed.

It has already been stated that *Andropogon furcatus* regularly forms an important element in the little bluestem type. *Sorghastrum nutans* is likewise found here, having also migrated up the ravines and become widely scattered over the broad drainage areas that conduct run-off water. Even on high crests and flat hilltops it may constitute locally 5 to 25 per cent of the vegetation. Southward it often ranks closely to *A. furcatus* in importance in the little bluestem type, but northward it is usually much less abundant and is often almost absent.

Bouteloua curtipendula occurs frequently but is usually of minor importance. *Elymus canadensis* and *Panicum virgatum* are found only where local disturbance has temporarily afforded an increased water supply. They are never abundant, in fact they are almost rare in all upland types except *Panicum virgatum* in the southern part. *Stipa spartea, Koeleria cristata,* and *Sporobolus heterolepis,* which will now be described, occur not only frequently but also often abundantly in this extensive upland consociation. The characteristic forbs of the little bluestem and other upland types are, in the main, rather distinct from those of the more moist lowlands. In general they are also of smaller stature.

Needle Grass Type
(Stipa spartea Consociation)

Stipa spartea Trin. is the chief dominant of a second upland type of prairie (Fig. 33). This bunch-forming grass is of practically no importance in the Kansas and Missouri section and is of minor importance in the south-

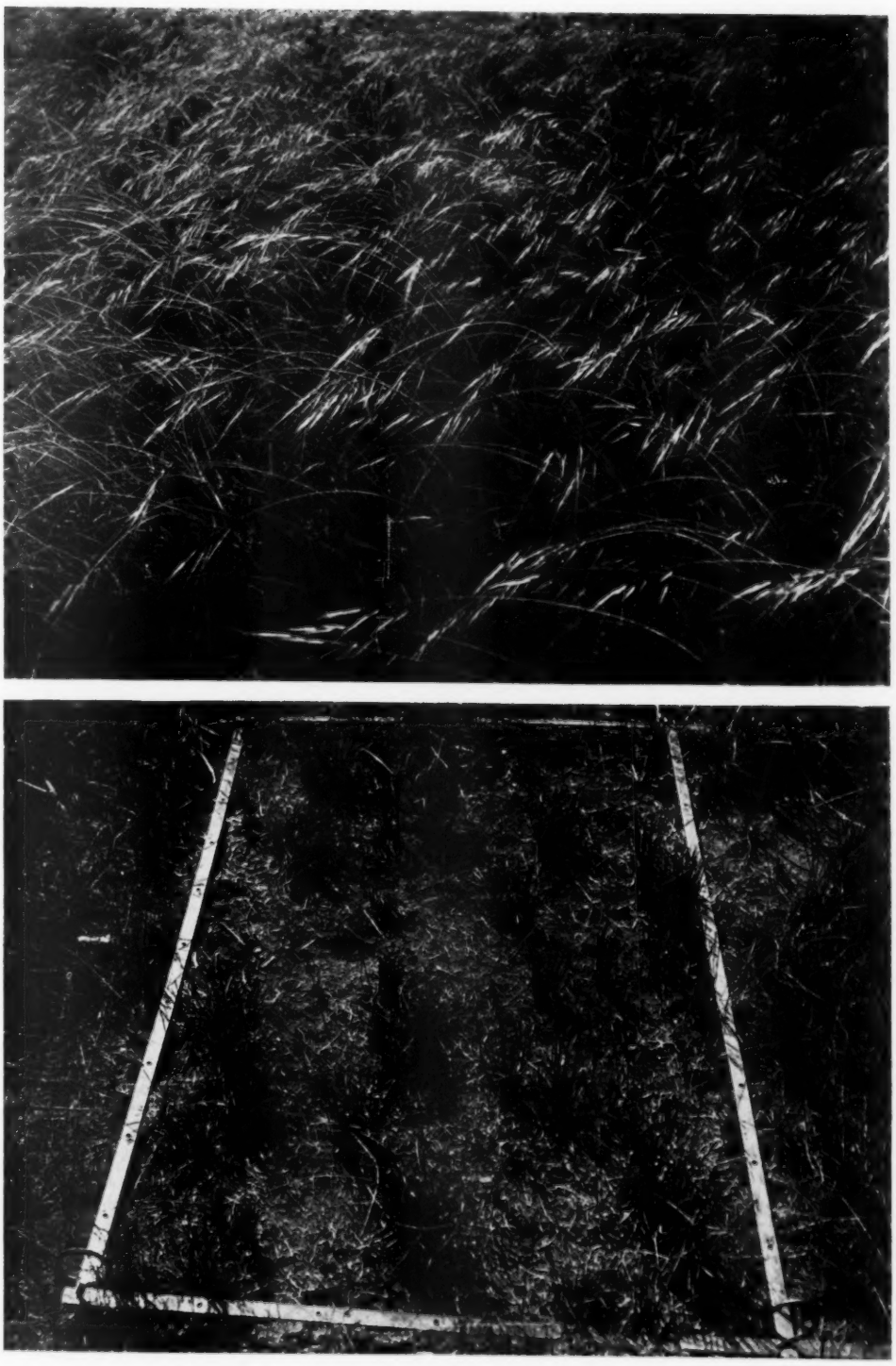

FIG. 33. Consociation of *Stipa spartea;* the flower stalks are bent under the weight of the seed. Photo. June 10.

FIG. 34. Representative bunches of *Stipa spartea* in one-half square meter near Ponca, Nebr. The spreading tops have been removed revealing the small basal cover.

eastern portions of the prairie area. But it gradually increases northward and the type becomes well developed. In Dakota, north of the area studied, needle grasses are the chief dominants over vast areas. Steep, dry ridges and xeric slopes, especially where the soil is thin and perhaps sandy or gravelly, are frequently more or less dominated by it. Such areas alternate with the little bluestem pattern or with that of *Sporobolus heterolepis*. The chief associates of needle grass are the bluestems and June grass (*Koeleria cristata*), but it is found in various groupings.[3]

Because of a greater height than most upland species, a rapid early growth, and the production of flower stalks early in June, together with its long leaves and very widely spreading top, Stipa frequently appears to dominate areas where it actually constitutes only 15 to 35 per cent of the vegetation. The foliage varies in height from 14 to 36 inches and the flower stalks are 3 to 4.5 feet tall. While the bases of the bunches are usually only 1 to 5 (but sometimes 12) cm. in diameter, the stems spread so widely, especially when ladened with the large, heavy, long-awned fruits, that the lateral spread of tops is often 1 to 3 feet.

In hilly lands in the central and northern parts of the area alternes of Stipa may cover one-fifth to one-third or even more of extensive uplands. Here it may locally comprise 50 to 80 per cent or even more of the plant cover. Moreover, it is frequently more or less abundant on flat lands at the heads of draws and is readily distributed over broad washes on lower slopes that are subject to overflow and deposit during exceptionally heavy rains. Here it is found with the big bluestem, usually in no great abundance, but sometimes dominating rather extensive local areas.

Where Stipa is fairly thick, the basal cover is very open and the greater the apparent density of the species the more the bare soil. This results from the smaller amounts of little bluestem and other less conspicuous elements. Frequently the basal cover is only 7 to 9 per cent; but it is usually about 11 (Fig. 34).

The yield of dry matter per square meter is very similar to that of little bluestem, about 350 to 400 grams, since the heavier flower stalks compensate a somewhat more open foliage cover.

The ability of Stipa to dominate or successfully compete on thin, dry soils is due partially to its excellent method of planting the seeds deeply in contact with moist soil; partly to its excellent and rapidly developed root system; but perhaps largely to its early growth, by means of which it avoids excessive competition.

Koeleria cristata (L.) Pers. is a common component of the needle-grass type, but it is also found in other types of uplands as well as on well drained lowlands. It is one of the ten most important grasses of the prairie. It is

[3] According to Pound and Clements (1900) and correspondence with Clements (1932) not only was *Stipa spartea* formerly more abundant, but also *Sporobolus asper* was far more important than this detailed survey reveals them to be at present.

a bunch grass but of smaller stature than any of the preceding. Like Stipa it is of boreal origin and is abundant in the northern part of the area. In many of the prairies southward Koeleria may be scarcely, if at all, represented but it usually forms 1 to 3 per cent of the upland cover, at least locally. An abundance greater than 5 to 10 per cent has rarely been found except in disturbed places.

The bunches vary from 1 to 12 cm. in width, although 4 to 5 cm. is an approximately average size. Where it is most abundant 15 to 20 tufts, varying in size from single plants to bunches with 10 to 30 stalks, may occur per square meter. The plants are very leafy at the base, the foliage 12 to 15 inches tall, and the flower stalks, which reach full development early in June, are 20 to 30 inches high. After midsummer the stems and cauline leaves wither and die. This may result in part from the root system which, although fine and well developed, is only about 15 inches deep.

Various other grasses common to the little bluestem type, including *Poa pratensis*, are found here, although in general they are less abundant and more poorly developed since this is a drier upland consociation. In general, the forbs are the same as those found associating with the little bluestem, but some of the less xeric ones are absent and others occur in less abundance. This type may be rather sharply delimited from that of the little bluestem with which it is mostly in contact but more usually the transition from one to the other is not abrupt. Hence, unless much care is exercised the actual territory occupied by the taller dominant is apt to be overestimated. Needle grass forms alternes not only with little bluestem but also less extensively with *Sporobolus heterolepis*.

PRAIRIE DROPSEED TYPE
(Sporobolus heterolepis Consociation)

A very minor but quite distinct upland pattern is exhibited by *Sporobolus heterolepis* A. Gray. This dropseed is distinctly a bunch former. Notwithstanding the wide distribution of the species over the area, it was not found in many of the prairies. It is always most abundant on the driest uplands where it may dominate local areas, forming 80 per cent or more of the vegetational cover. The areas over which it holds control are much less extensive than those of the Stipa type. They vary from a few acres to a few square rods in extent and all degrees of intermingling with the needlegrass type and the little bluestem type occur. Usually Sporobolus occurs as scattered bunches intermingled with *Stipa spartea* and *Andropogon scoparius* where it constitutes anywhere from 1 to 20 per cent of the cover. From the hilltops and dry upper slopes it sometimes migrates downward and isolated clumps occur even in areas dominated by *Andropogon furcatus*.

The bunches are usually 4 to 7 inches in diameter but much larger ones may occur. The stems vary from 50 to over 200 per sq. dm. and invasion of

the bunch rarely occurs. The foliage of narrow, long, attenuated leaves reaches a level of 8 to 18 inches, depending on the water supply, and the spreading panicles, which develop in late summer and autumn, 1.5 to 3 feet. Although the basal cover in this type is usually only 8 to 15 per cent, the widely spreading foliage obscures the bare places between the bunches and the sod-like, smaller tufts. Hence, in areas of nearly pure Sporobolus, where the foliage cover is 80 to 90 per cent, the basal area is actually about 12 per cent. Underground, however, the whole soil mass is preëmpted by roots. Once in possession it keeps its holdings against all invaders for long periods of time. Forbs are not plentiful where this consociation is well developed and, in general, they represent the more xeric ones found regularly on uplands.

DISTRIBUTION OF THE MAJOR GRASSES WITHIN THE SEVERAL CONSOCIATIONS

Variations in the plant cover result from topography which affects especially the water content of soil and humidity of the atmosphere. Typical variations will be illustrated by a series of quadrats selected from different and widely separated prairies. For the sake of simplicity, only the more important grasses are listed. Their abundance is expressed in per cent of the total ground cover.

ANDROPOGON SCOPARIUS AND A. FURCATUS CONSOCIATIONS

Table 1 shows the change in plant cover as one proceeds from the top of a westwardly facing slope to the foot of a rather steep hill at Ida Grove, Iowa (Fig. 35). These are the actual data obtained in the field and are presented first because of the almost perfect transitional sequence.

TABLE 1. *Quadrats from near Ida Grove, Iowa, July 25, 1930.*

Species	Hilltop	Upper Slope			Midslope		Lower Slope		Level base
Andropogon scoparius	70	70	56	44	44	40	..	..	..
Andropogon furcatus	13	22	27	35	35	40	75	80	97
Poa pratensis	7	3	10	10	10	5	5	15	1
Stipa spartea	2	..	1	..	..	4	4	..	.
Basal cover (per cent)	25	21	17	15	15	15	13	11	10

Even casual examination of Table 1 shows the dominance of little bluestem on the upland and its gradual decrease toward the lower slope where it is entirely replaced by big bluestem. The gradual increase of the latter from hilltop to valley is quite as characteristic as is the persistence of bluegrass, which forms an understory in both types. The percentage of Stipa is characteristically small. It may be noted that 84 to 98 per cent of the basal cover of vegetation is represented by these four species of grasses and 75 to

97 per cent by the two dominants alone. There is an unusual uniformity in the decrease of the percentage of basal cover in this series from the upland to the big bluestem type. The average height of the little bluestem ranged

FIG. 35. Portion of upland prairie near Ida Grove, Ia. *Ceanothus pubescens* conspicuous in foreground.

FIG. 36. Detail of *Andropogon scoparius* type near Guthrie Center, Ia., June 14. *Amorpha canescens* and *Helianthus rigidus* are the most important forbs.

from 9 to 11 inches; the big bluestem increased from 14 inches on the hilltop to 21 inches at its base.

A second series of quadrats, taken during the middle of June of the same year, are from Harlan and Guthrie Center. These stations, like the preceding, are in west central Iowa (Fig. 36).

TABLE 2. *Quadrats from a north slope near Harlan and a south slope near Guthrie Center, Iowa.*

Species	Level upland	Hill crest	Midslope		Lower slope	Midslope		Lower slope	
Andropogon scoparius	20	90	57	..	..	89	90	48	46
Andropogon furcatus	71	5	33	94	95	3	5	47	48
Poa pratensis	5	2	2	5	3	2	..	2	5
Basal cover (per cent)	14	29	26	17	26	20	19	17	18

A new fact is revealed by the first quadrat, namely that on a level upland where run-off is little or none, big bluestem often is found in abundance. Conversely, little bluestem often dominates or shares equally with its big competitor on lower slopes of steep xeroclines, that is on south and southwest slopes. Otherwise the same principles of distribution are shown as by the preceding series. The height of *A. scoparius* was rather consistently about 12 inches; that of *A. furcatus* increased in the first series from 10 to 15 inches. The basal cover was somewhat greater in these quadrats than the average for the prairie region as a whole.

Proceeding 130 miles westward to Wisner and Valparaiso, Nebraska, the data in Table 3 were obtained (Fig. 37).

TABLE 3. *Series of quadrats from a long west slope at Wisner, and a steep north slope at Valparaiso, Nebraska, August 1, 1930.*

Species	Upper slope				Lower midslope			Lower slope				Hill-top	Upper slope	Lower slope	
Andropogon scoparius	47	62	38	32	..	..	..	..	..	..	..	61	50	..	..
Andropogon furcatus	10	15	8	48	75	74	77	89	92	86	89	9	37	86	97
Poa pratensis	12	12	30	10	15	14	15	5	3	10	5	3	5	10	2
Bouteloua gracilis	..	..	..	..	..	..	..	..	..	..	..	20	..	..	..
Basal cover (per cent)	13	16	13	..	..	11	..	..	..	..	9	18	13	13	19

These quadrats again show the dominance of little bluestem on the drier uplands and that of big bluestem on soils that receive run-off water from the upper slopes. In the first series, measured on August 1, *Andropogon scoparius* increased from 8 to 10 inches in height and *A. furcatus* from 12 to 17 proceeding down the hill. It is an interesting fact that the distribution of big bluestem is much more general over many prairies than is that of its smaller

competitor. The latter often entirely disappears on low ground; big bluestem is found, at least in small amounts, in nearly every upland area. At Valparaiso (July 5) the increase was from 7 to 9 and 12 to 26 inches for the two bluestems respectively. The presence of *Bouteloua gracilis* indicates both the position of the prairie in the western portion of the general area and a thin soil. The foliage cover in the four quadrats from hilltop to lower slope was approximately 50, 70, 90, and 100 per cent, respectively.

A final group of similar quadrats from near Topeka, Hoyt, and Onaga in northeastern Kansas are shown in Tables 4 and 5.

TABLE 4. *Series of quadrats from near the top to the base of a long, rather gentle south slope near Topeka, July 19, 1930.*

Species	Upper slope				Mid-slope		Lower slope		Level base	
Andropogon scoparius	65	40	81	69	52	75	15	18	16	5
Andropogon furcatus	10	9	10	8	30	20	63	60	80	89
Sporobolus heterolepis	15	50	..	..	6	..	..	..	..	..
Panicum virgatum	..	..	2	8	10	4	..	5	2	..
Foliage cover (per cent)	50	50	50	60	75	80	90	100	100	100
Basal cover (per cent)	14	10	13	15	12	18	13	13	15	13

TABLE 5. *Series of quadrats taken at intervals down a west slope and up an east one at Onaga; and down a north slope at Hoyt, Kansas, July 20, 1930.*

Species	Upper slope		Lower slope	Level base		Mid-slope	Hill crest	Level top	Down north slope			
Andropogon scoparius	78	60	15	..	..	40	66	66	91	76	61	75
Andropogon furcatus	15	30	70	75	88	46	10	18	5	7	20	23
Sorghastrum nutans	2	4	5	2	5	5	..	1	1	5	5	..
Koeleria cristata	..	..	..	..	..	..	..	1	..	8	..	..
Poa pratensis	..	..	5	20	5	5	..	1	..	..	..	..
Basal cover (per cent)	12	11	12	19	17	17	16	17	17	17	19	16

The prairie near Topeka shows a general decrease of little bluestem proceeding down the long slope as well as the persistence of this grass even at the foot. A reciprocal distribution is shown by big bluestem. This series also included an alterne of Sporobolus on the upper slope, and a rather heavy sprinkling of somewhat dwarfed *Panicum virgatum*. As has been pointed out, Panicum is more abundant southward. The foliage cover shows a progressive increase from upland to low ground, although, as usual, the basal cover exhibits no such change. The four species of grasses alone furnish 78 to 99 per cent of the basal cover. The foliage cover at Topeka ranged from 50 to 60 per cent on the upper slope, 75 to 80 on the midslope, and 90 to 100 on the lower slope and level base. Little bluestem increased in average height

from 11 to 17 inches and big bluestem from 17 to 22 as the water content became higher and aerial environment less severe on the lower ground.

The quadrats in Table 5 confirm the usual distribution as well as the over-

FIG. 37. Upland prairie near Wisner, Nebr., with an abundance of *Psoralea argophylla*. Photo. June 10.

FIG. 38. Lowland prairie with an abundance of *Asclepias sullivantii;* typical of the lowland near Havelock and Columbus, Nebr. Photo. July 15.

whelming importance of the two bluestem grasses. Here, as is usual southward, Sorghastrum is found more or less throughout. As before, no consistent differences are shown in the percentage of basal cover.

A number of quadrats in the *Andropogon furcatus* type is shown for both the wetter and drier portions of the area in Tables 6 and 7 (Fig. 38).

TABLE 6. *Quadrats from rather low level "second bottom" prairies near Tarkio and Bigelow, Mo., June 27 and 28, 1930.*

Species	Nearly level land					Level land		
Andropogon scoparius	..	..	..	..	..	..	..	..
Andropogon furcatus	90	84	88	63	95	98	93	90
Sorghastrum nutans	..	..	1	..	..	..	1	..
Poa pratensis	1	1	2	..	2	1	2	..
Panicum virgatum	..	..	1	..	1	..	1	5
Basal cover (per cent)	16	11	19	37[a]	25	14	20	14

[a]The high percentage of basal cover was due to an abundance of *Antennaria campestris*.

TABLE 7. *Quadrats from low, nearly level prairies near Havelock and Columbus, Nebr., July 1-8, 1929.*

Species	Nearly level land								Nearly level land								
Andropogon scoparius	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Andropogon furcatus	65	67	33	95	86	95	87	79	66	78	92	82	84	80	90	86	95
Sorghastrum nutans	30	25	54	2	..	..	..	..	..	..	..	..	..	..	..	..	..
Poa pratensis	3	3	5	3	8	3	10	15	10	5	..	10	..	1	..	6	2
Panicum virgatum	1	..	..	..	3	2	2	5	2	..	..	..	..	..	..	..	1
Spartina michauxiana	..	..	..	..	..	..	..	..	10	10	2	..	3	..	..	..	..
Basal cover (per cent)	12	9	13	10	13	11	12	8	..	..	..	..	..	..	..	..	..

The small percentage of Poa at the Missouri stations is correlated with the excellent cover of big bluestem which on June 27 had already attained a height of 22 to 28 inches and densely shaded the soil. The large amount of Sorghastrum in the prairie near Havelock is not typical and was due to an oxbow loop in the stream which during exceptionally high water resulted in overflow. Further illustrations seem unnecessary to show the complete dominance and great abundance of big bluestem in well drained lowlands as well as on lower moist slopes.

STIPA SPARTEA CONSOCIATION

Series of quadrats from the northern parts of the area which show the distribution and abundance of Stipa are given in Tables 8 to 10.

TABLE 8. *A series of quadrats from high, nearly level land, over the brow of a hill, and from midslope to lower slope near Cherokee, Iowa, July 26, 1930.*

Species	Level upland				Brow of hill				Midslope				Lower slope	
Andropogon scoparius	67	62	51	69	61	44	30	15	40	15	35	50	18	11
Andropogon furcatus	5	25	35	10	10	15	15	12	33	58	33	29	70	70
Stipa spartea	5	8	5	10	15	30	48	45	8	10	..	3	..	3
Poa pratensis	5	2	1	3	3	2	5	8	2	8	5	5	1	5

TABLE 9. *Quadrats from lowland up a hill through an alterne of Stipa on its brow to level upland. Spencer, Iowa, July 25, 1930.*

Species	Lowland to lower midslope				Stipa alterne		Upper slope			Level upland		
Andropogon scoparius	..	..	30	42	36	40	70	75	79	60	72	79
Andropogon furcatus	85	78	47	40	10	15	15	4	5	30	25	10
Stipa spartea	..	..	..	2	37	27	..	8	10	..	..	10
Poa pratensis	2	10	20	15	15	15	12	5	1	..	1	1
Basal cover (per cent)	10	15	12	13	13	8	19	14	14	15	18	14

Table 8 shows the dominance of little bluestem on the level upland, although there is a good admixture of big bluestem. Little bluestem decreased in the alterne of needle grass on the brow of the hill, shared dominance with big bluestem on the midslope, and gave way to the taller dominant on the lower slope. The general admixture of needle grass and bluegrass over the area is characteristic of these northern prairies. Only a few species constitute the bulk of the vegetation. The basal cover varied from 9 to 13 per cent.

The quadrats near Spencer indicate a situation that frequently is found; namely, the alterne of Stipa occupying the steepest part of the hill where run-off and erosion are greatest, and the dominance of the bluestems both above and below. The increase of big bluestem on the level hilltop is also significant. Here it was only 10 to 12 inches tall as compared with 15 to 17 on lower ground. Stipa was 18 to 22 inches high. The usual decrease in ground cover in the alterne of Stipa is not shown because of an unusual abundance of Poa.

A series of quadrats were obtained near Allen in northeastern Nebraska, where the two bluestems constituted 76 to 94 per cent of the grasses except in the alternes of Stipa (Fig. 4). The unit areas represent samples of the vegetation in a belt extending from the base, up the east slope, to the top of a high, wind-swept hill.

TABLE 10. *Series of quadrats near Allen, Nebraska, made on August 2, 1930. The two lower lines indicate the average height of the grasses in inches.*

Species	Lower midslope				Stipa ridge			Upper slope				Gently sloping hilltop			
Andropogon scoparius	..	..	..	..	..	5	..	69	70	65	62	77	89	76	79
Andropogon furcatus	77	81	76	80	65	24	40	25	15	15	15	10	5	8	5
Stipa spartea	5	10	10	1	20	45	50	..	3	2	10	3	..	..	..
Poa pratensis	8	5	5	5	5	5	6	2	4	5	10	5	1	5	3
Andropogon scoparius	..	..	..	..	..	10	..	10	11	9	7	8	6	6	6
Andropogon furcatus	19	18	18	18	20	17	16	..	..	15	13	11	8	9	8

It is a significant fact that although a small percentage of Stipa was scattered throughout this 100-acre prairie, the needle grass was dominant only along a wide belt following the steepest xerocline. There was very little on the long, north slope. The general absence of *Andropogon scoparius* and the high percentage of *A. furcatus* in the alterne is somewhat unusual. Poa is somewhat uniformly represented throughout although in small amounts.

Table 11 shows several quadrats from the thinner soil of hill crests in southeastern Nebraska, and also includes four quadrats showing the major composition of vegetation from the deeper, level, upland soil (Fig. 39).

TABLE 11. *Selected quadrats from the less extensive xeric alternes at Lincoln and Nebraska City, Nebraska, and from other typical upland areas.*

Species	Thinner soil on high ridges							Deep, fertile upland			
Andropogon scoparius	18	25	25	13	29	21	4	76	80	15	51
Andropogon furcatus	15	30	7	41	38	30	25	15	11	68	41
Stipa spartea	..	..	50	36	26	38	56	2	2	3	1
Poa pratensis	..	5	..	1	1	2	6	1	1	4	4
Sporobolus heterolepis	46	25	10	..	..	..	..	..	..	..	..

From these data, it may be seen that Stipa, even where best developed, frequently does not constitute one-half of the ground cover. The alternes of Stipa are far less extensive in this central portion of the area and farther southward the species all but disappears. Sporobolus, it may be noted, is less widely scattered but where it does occur it is frequently abundant.

GENERAL DISTRIBUTION

The distribution of the types of grassland and that of the dominant species may be illustrated further by selecting a few typical cases. On a long, west slope of a loess hill in northeastern Nebraska, the bluestem type prevailed. Near the base and on the lower slope, a nearly pure stand of big bluestem 22 inches tall composed with the forbs a foliage cover of 90 to 100 per cent. About one-third of the way up the hill the big bluestem had

decreased to 18 inches in height, and one-fourth in abundance. Little bluestem, 10 inches high, now constituted approximately 25 per cent of the basal cover. A little higher up the slope, an almost equal mixture of the two domi-

FIG. 39. Alterne of *Stipa spartea* in *Andropogon* prairie near Nebraska City. *Ceanothus pubescens* is conspicuous.

FIG. 40. Small society of *Artemisia gnaphalodes* taken on June 15 when the plants were about two feet high.

nants occurred, the larger one being reduced to 15 inches in height; a few forbs and a little bluegrass constituting the remainder of the 80 per cent cover of foliage. The big bluestem continued to form 15 to 40 per cent of the vegetation until the upper slope and rounded hilltop were reached. Here it was represented by only 1 to 5 per cent. Little bluestem increased correspondingly, from 70 per cent about two-thirds way up until it composed 90 or even 95 per cent of the basal cover. It formed a well developed sod-mat about 8 inches high with only a sprinkling of other grasses. The foliage cover, including forbs, varied from 70 to 85 per cent.

The distribution of dominants on the west slope was practically the same as on the other hillsides except that *Andropogon scoparius* ranged farther downward on the south slope, and *A. furcatus* farther upward on the north. Situations similar to the one described were observed in scores of prairies throughout the entire area. Where the land is less rolling transitions from one type to the other are less abrupt but they always occur wherever change in habitat factors is sufficient.

Where alternes of Stipa occur, the sequence is somewhat different. The bluestems then give way to needle grass on the crests of the hills where run-off is great and the soil often of a poorer type. Stipa may dominate the whole upper slope, but bluestems usually recur on the flat hilltop. Sometimes, however, depending upon conditions, they may also be more or less completely replaced here also by the Stipa or Sporobolus types. Because of the greater height of Stipa (3 to 4 feet) and the sparse foliage cover, as well as the very pronounced bunch habit and yellowish-green color of Sporobolus, these types are easily discernible, even at some distance. In general there is less bluegrass in these consociations; the forbs consist of the more xeric species; and they are frequently dwarfed. The local occurrence of alternes of Stipa in lower ground at the foot of draws, probably as a result of flooding, brings it into more direct contact with the big bluestem.

In certain places, and particularly in Kansas, where the underlying layers of rock outcrop, the sequence described for the bluestems is often interrupted. This is because it is not the topography directly that determines plant distribution, but only its influence upon the water content of soil through run-off, etc., and upon other factors of the habitat. Seepage along the edge of a horizontal ledge of rock covered with a few feet of soil may permit *Andropogon furcatus*, or even Spartina or Tripsacum, to form a zone of vegetation high up the slope and thus interrupt the usual sequence of the dominants. Conversely a similar layer of rock even on relatively low ground, if covered with only a little soil, may result in vegetation typical of upper slopes and hilltops. Over such an area the cover of vegetation is irregular in appearance, for not only does the height of the grasses vary abruptly but also that of the accompanying forbs.

Where the soil is especially thin, small alternes of the short grasses may

occur or these may continue some distance along the dry rocky outcrop, clearly delimiting its extent. The transition is often abrupt. A good growth of little bluestem, interspersed with big bluestem and Indian grass, gives way abruptly, as the soil becomes thinner, to a very open, dwarfed, and distinctly bunched type. This may be replaced almost completely by areas of *Bouteloua gracilis*, *B. hirsuta*, and *Bulbilis dactyloides*. Accompanying them are a few characteristic, xeric forbs and grasses. Chief among these are *Festuca octoflora*, scattered tufts of *Sporobolus asper* and *S. cryptandrus*, *Hedeoma hispida*, *Plantago purshii*, and sometimes species of Opuntia. Above this area of thinner soil the usual little bluestem type ordinarily prevails, although if the soil is deep and the precipitation sufficiently great it may share the level uplands with the more mesic big bluestem and Indian grass.

Transitions between the several lowland types are little affected by topography except as it determines the accumulation of run-off water and the depth of the water table. Consequently, although the types themselves are distinct, various mixtures occur.

ANALYSES OF THE VEGETATION IN THE SEVERAL GRASSLAND TYPES

Numerous samples of the vegetation, each consisting of one square meter, were taken in the six states in the several types of grassland. These were used to determine the average percentage composition of the vegetation. Their significance is greatly enhanced by the fact that the data disclosed by their analyses were confirmed by literally hundreds of critical and detailed observations in the 135 prairies in which these studies were made.

ANDROPOGON SCOPARIUS CONSOCIATION

Quadrats made in the little bluestem type alone aggregated 180. The average basal cover of vegetation (from 138 quadrats) was only 15.3 per cent.[5] In 17 quadrats it fell to less than 10 per cent, with a minimum of 6.5. It exceeded 20 per cent in 20 quadrats and reached a maximum of 29 per cent.

Little bluestem occurred in all of the 180 quadrats, save three, and furnished an average of 55 per cent of the basal cover. Only in 20 per cent of the unit areas did it constitute less than 40 per cent of the vegetation and in 31 it exceeded 70 per cent. In 21 quadrats this species represented less than 20 per cent of the cover, while in 12 it exceeded 85 per cent. In seven of the 12 it alone furnished from 90 to 98 per cent of the basal cover.

Big bluestem furnished on an average 24.8 per cent of the total basal cover. This large amount was due not only to the fact that this species was quite as constant as the preceding but also that it was of considerable abundance especially on lower midslopes and on well watered, less rolling

[5] It is of interest to note that the sod-forming *Bouteloua gracilis* and *Bulbilis dactyloides* in adjacent native pastures had a basal cover varying from 50 to over 80 per cent.

upland areas. Hence, a wide range in its percentage of the total basal cover in the various quadrats may be anticipated. Some of these quadrats, moreover, included transitional areas between the big and little bluestem types. In 15 per cent of the unit areas the percentage of the total basal cover due to this species ranged from 1 to 5; in 16 per cent from 6 to 10; and in 13 per cent from 11 to 15. Moreover, it constituted between 40 and 50 per cent of the basal cover in 12 per cent of the quadrats and exceeded this percentage in only 15 unit areas. In two of the latter it constituted 84 and 91 per cent of the entire cover.

The two bluestems together constituted 80 per cent of the entire plant cover. The rôle played by the closely related *Sorghastrum nutans* is one of very minor importance (Table 12). Its wide distribution is shown by the fact that it was found in over one-half of the quadrats, just as its sparseness is illustrated by its small proportion (1.8 per cent) of the basal plant cover. In only about 6 per cent of the quadrats did it exceed 5 per cent; the maximum was 29.

TABLE 12. *Percentage of basal cover in Andropogon scoparius type composed of various grasses and forbs, and percentage of quadrats in which each occurred. First section, 180 quadrats throughout the area; second section, 130 quadrats in the drier part of the area; third section, 50 quadrats from the wetter part.*

Species	Per cent cover	Per cent occurrence	Per cent cover	Per cent occurrence	Per cent cover	Per cent occurrence
Andropogon scoparius	55.0	98	56.2	99	51.7	96
Andropogon furcatus	24.8	99	23.1	99	29.3	98
Poa pratensis	4.7	80	5.8	94	1.7	43
Stipa spartea	2.5	40	3.1	49	1.1	16
Sporobolus heterolepis	2.7	20	2.8	22	2.3	16
Sorghastrum nutans	1.8	51	1.4	49	3.0	57
Bouteloua curtipendula	.6	32	.7	37	.5	18
Panicum scribnerianum, P. wilcoxianum	.4	36	.3	34	.5	43
Koeleria cristata	.6	34	.6	39	.4	22
Elymus canadensis	.0	4	.0	5	.0	2
Panicum virgatum	1.3	14	0.1	5	4.6	37
Forbs	4.1	90	4.2	89	3.7	92
Total	98.5	..	98.3	..	98.8	..

Stipa spartea and *Sporobolus heterolepis* each constituted about 2.5 per cent of the ground cover. The distribution of Stipa was much more regular than that of Sporobolus, since the latter occurred in only one-half as many quadrats (20 per cent) as Stipa. Stipa exceeded 10 per cent in ground cover in only 8 quadrats, Sporobolus in 17. Quadrats where either of these species formed 25 or more per cent were only 5 and 6 respectively, a maximum of 36 per cent of the cover being formed by Stipa in one case.

Koeleria cristata, *Bouteloua curtipendula*, and the smaller panic grasses (*Panicum scribnerianum* and *P. wilcoxianum*) each constituted approximately 0.5 per cent. Moreover, their percentage occurrence in the quadrats was nearly the same, about 35. Thus all three are widely distributed but rarely occur in abundance. The largest amounts found in any quadrat were, in the above sequence, 8, 10, and 3 per cent.

Elymus canadensis is almost negligible since it was found in only 4 per cent of the quadrats and never greater in amount than 1 per cent.

Panicum virgatum had likewise a limited occurrence on the uplands (14 per cent), but constituted a large proportion of the cover (30-62 per cent) in several quadrats in the southeastern section of the area. Extensive field studies bear out this relationship.

The very wide distribution and great abundance of *Poa pratensis* are of much importance. Occurring in 80 per cent of the unit areas and constituting 4.7 per cent of the plant cover, it ranks as the third most abundant species of grass. Frequently it constituted only 1 to 2 per cent of the cover, in 54 per cent of the quadrats it was 5 per cent or less, and in 14 per cent 6 to 10. In 10 per cent it ranged between 11 and 20 and in only 3 quadrats was it more abundant, maximum 30 per cent. Thus although this species is usually hidden below the general cover of grasses after the middle of June, yet in the early part of the season it plays an important rôle. On the basis of dry weight of forage production its rank would be much lower.

Forbs, notwithstanding their abundance and conspicuousness, constituted an average of only 4 per cent of the basal cover although they occurred in 90 per cent of the quadrats (Fig. 40). In many of the unit areas they represented only 1 or 2 per cent of the ground cover and exceeded 10 per cent in only 7 instances. A maximum cover of 15 per cent was found. In this connection it should be emphasized that typical quadrats only were used and not those representing extreme conditions of abundance of forbs or any other species (Fig. 41). Repeated close study, supplemented by numerous more general surveys, bears out the facts here obtained. Although the forbs may often seem far more important, and in some cases actually are so, yet as regards their part of the basal cover, the percentage rarely averaged much more than 5 to 12. It must also be kept clearly in mind that even the grasses, often with a foliage cover of 100 per cent, actually clothe, on an average, only about 15 per cent of the surface of the soil.

Examination of Table 12 shows that 98.5 per cent of the entire basal cover is due to a dozen grasses and the forbs, the remaining fraction being composed of minor grasses and sedges.

A comparison of 130 quadrats of the uplands in the drier area with 50 from the prairies with a precipitation in excess of 32 inches annually (Table 12) shows certain differences, all of which were verified by the extensive field studies.

There is an increase of over 5 per cent in basal cover in the less arid section, i.e., from 15 to 15.8 per cent average basal cover. As regards the percentage of the basal cover furnished by the dominant species, *Andropogon scoparius*, decreased from 56.2 to 51.7, while *A. furcatus* increased from 23.1 to 29.3 per cent. This illustrates the delicate balance between these species and how the taller grass encroaches upon the territory of the shorter one where water content of soil becomes more abundant. It is significant

FIG. 41. Society of *Solidago glaberrima*, Harrisburg, S. Dak., June 12. This is one of the most important forbs of the prairie.

FIG. 42. Low prairie near Vermilion, S. Dak., showing extensive (dark) alternes of *Juncus tenuis*. The conspicuous forb is *Apocynum sibiricum*.

that the two competitors were present in practically every quadrat in both areas.

The tendency of Sorghastrum to increase is also clearly evident. Its percentage of ground cover is more than doubled and its representation in the quadrats increased by 16 per cent. The coarse *Panicum virgatum*, although rarely abundant, showed a marked increase. From 0.1 per cent of the basal cover it increased to 4.6, and in occurrence from 5 to 37 per cent.

A considerable decrease occurred in both Koeleria and Bouteloua in the number of quadrats in which they were represented—the former from 39 to 22 per cent; the latter from 37 to 18. The decrease in both the amount and distribution of Stipa was marked. From a cover percentage of 3.1 it fell to 1.1 and its occurrence in half of the quadrats fell to 16 per cent. The small panic grasses showed a slight increase and Sporobolus a decrease. No significant change occurred in the case of the forbs, but there was a marked decrease in abundance and uniformity of distribution of bluegrass. From 5.8 per cent of the cover it fell to 1.7, and its presence in 94 per cent of the quadrats to only 43. This is undoubtedly due to the better development of the taller grasses and forbs in the area of higher precipitation. Where these are handicapped, as for example by grazing, the bluegrass greatly increases. In fact, grazing may be so regulated that an almost complete stand of the bluegrass may result which, in northern Missouri, is allowed to fruit and is then "stripped" by mechanical "strippers" for the seed.

ANDROPOGON FURCATUS CONSOCIATION

An analysis of a group of 155 quadrats made throughout the area in the typical *Andropogon furcatus* type reveals a number of important facts. The basal cover of vegetation average 13.3 per cent in 103 quadrats. It was less than 8 per cent in only 11 quadrats, the least cover being 4.8 per cent. But it exceeded 15 per cent in 21 square meters. A maximum cover of more than 20 per cent was found in only three quadrats, one of these, because of a dense growth of *Antennaria campestris*, reaching 37 per cent.

The big bluestem constituted 78 per cent of the vegetation [illegible] presented in every quadrat. Its great abundance is shown by the fact [illegible]at in 32 per cent it ranged between 80 and 89 and in 22 per cent of the quadrats it constituted 90 per cent or more of the basal cover. In 17 cases it composed 95 to 98 per cent of the entire vegetation. It was less than 60 per cent in but 14 quadrats and below 40 per cent (minimum 20) in only 5. Thus it is truly the great dominant of lowlands.

Andropogon scoparius constituted only 2 per cent of the plant cover and was found in about 19 per cent of the quadrats. Its percentage in these ranged between 2 and 31 (Table 13).

TABLE 13. *Percentage of basal cover in Andropogon furcatus type composed of various grasses and forbs and percentage of quadrats in which each occurred. First section, 155 quadrats throughout the area; second section, 133 quadrats in the drier part of the area; third section, 22 quadrats in the wetter part of the area.*

Species	Per cent cover	Per cent occurrence	Per cent cover	Per cent occurrence	Per cent cover	Per cent occurrence
Andropogon scoparius	2.0	19	1.9	19	2.9	18
Andropogon furcatus	78.0	100	78.3	100	75.9	100
Poa pratensis	8.8	88	9.7	93	3.1	64
Stipa spartea	1.9	31	2.2	35	.2	9
Sporobolus heterolepis	.1	1	.2	2	.0	0
Sorghastrum nutans	1.9	37	2.1	37	.9	36
Bouteloua curtipendula	.1	7	.1	8	.0	0
Panicum scribnerianum, P. wilcoxianum	.3	28	.3	29	.3	27
Koeleria cristata	.1	10	.1	12	.0	0
Elymus canadensis	.1	12	.1	12	.1	9
Panicum virgatum	1.7	22	.6	16	8.1	59
Spartina michauxiana	.4	12	.3	10	.6	23
Forbs	3.6	74	3.0	70	7.1	100
Total	99.0	..	98.9	..	99.2	..

Poa pratensis was represented in all but 12 per cent of the unit areas and constituted 8.8 per cent of the basal cover. In 25 per cent of the quadrats where it was found it made less than 5 per cent of the cover and in 14 per cent more than 15. Maxima of 32 and 35 per cent were found in two quadrats.

Stipa spartea afforded slightly less than 2 per cent of the cover and occurred in less than one-third of the quadrats. In only 4 did it exceed 10 per cent and in 16 others was represented by one or less than one per cent.

Sporobolus heterolepis and *Bouteloua curtipendula* were almost negligible both as regards the percentage composition and the number of quadrats in which they occurred. The same is true of *Koeleria cristata, Elymus canadensis,* and *Spartina michauxiana* as regards percentage composition, although they were found in 10 to 12 per cent of the quadrats. In only one case did Koeleria exceed 2 per cent in any quadrat; Elymus never constituted more than 3 per cent of the cover; Spartina made 5 per cent in only 2 quadrats.

Panicum virgatum was distributed in about one-fifth of the unit areas and constituted an average basal cover of less than 2 per cent. In only 4 of these quadrats did it exceed 20 per cent and was usually 1 to 5.

Sorghastrum nutans was slightly more abundant, occurring in 37 per cent of the quadrats and furnishing about 2 per cent of the cover. In only 6 unit areas did it constitute more than 10 per cent of the vegetation and although it composed one-third to more than one-half in a very few cases yet the usual percentage where it occurred was 1 to 3.

Panicum scribnerianum and *P. wilcoxianum* were found in only about one quadrat out of four and with one exception never furnished more than 1 per cent of the cover of vegetation.

The forbs were listed in three-fourths of the quadrats and the total basal cover furnished by them average 3.6 per cent.[6] In 58 per cent of the quadrats where forbs were found, they formed less than 5 per cent of the cover and exceeded 10 per cent (maximum 35 per cent) in only 10 per cent (Figs. 43 and 45).

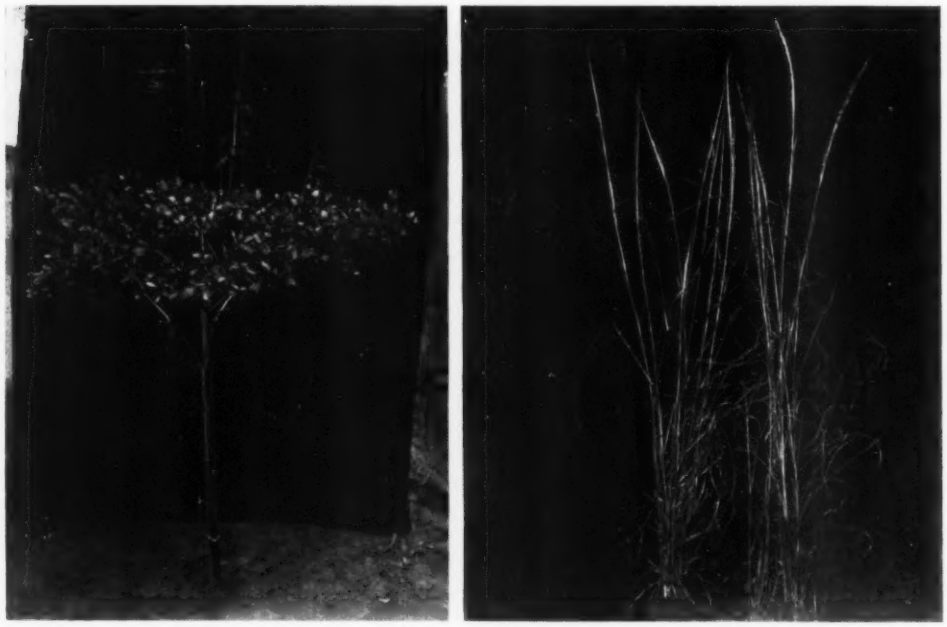

FIG. 43. *Baptisia leucantha* with single stem (attached to meter stick) which holds the spreading crown far above the grasses. Height of inflorescence about 5 feet. Photo. Sept. 25.

FIG. 44. Two characteristic clumps of *Sporobolus asper*, about 3 feet high. Photo. Sept. 15.

When the low prairie quadrats of the drier area are contrasted with those of the part of the prairie receiving more than 32 inches of precipitation (Fig. 3), some important differences are disclosed. The average basal cover increased about 9 per cent under the higher rainfall, i.e., from a total of 13 in the drier section to 14.2. The percentage of cover due to *Andropogon furcatus* changed from 78 to 76, the difference being in part compensated by an increase from 1.9 to 2.9 in *A. scoparius*. This change is of little importance since the first species was found in all the quadrats and the latter in only about 18 per cent in both cases.

Panicum virgatum, which is of southern origin, increased from 0.6 to 8.1

[6] In quadrating, the total basal cover, although it might be only 15 per cent, was considered as unity (100). Unless the basal cover afforded by any species or by forbs exceeded 0.5 per cent in any quadrat, it was not included.

per cent as regards basal cover and from 16 to 59 in percentage occurrence in the total number of quadrats.

A marked increase in the part of the basal cover due to forbs may be noted. In the dry area this was 3.0 per cent, where they were found in 70 per cent of the quadrats, as against 7.1 per cent (occurrence in all of the units) in the area of greater rainfall, where there occurred a larger margin of water in excess of that used by the grasses.

Stipa spartea, a species of boreal origin, decreased in basal cover from 2.2 to only 0.2 per cent. Its occurrence in 35 per cent of the quadrats of the drier area was reduced to 9 per cent in the wetter one.

Three grasses, Koeleria, Sporobolus, and Bouteloua, did not occur in any of the quadrats of the wetter area. Because of the greater stature of the plants and consequently reduced light intensity near the surface of the soil, *Poa pratensis* also showed a marked decrease. Its partial cover fell from 10 to 3 per cent and its occurrence from 93 to 64 per cent.

It should be emphasized that all of these differences shown by the quadrats were found to agree with the general field studies conducted throughout the prairies.

STIPA SPARTEA CONSOCIATION

An analysis of 25 representative quadrats in the *Stipa spartea* type, which is found only in the drier area, shows that the dominant grass constituted over 51 per cent of the cover and was represented in every quadrat. In only 4 quadrats did it fall below 40 per cent (minimum 30) and in 3 others it ranged from 74 to 80 per cent.

The basal cover was only about two-thirds as great (10.9 per cent) as in the little bluestem type. A minimum of 8.6 and a maximum of 13.7 were found.

The bluestems were the next most important species; *Andropogon furcatus* with 17.5 per cent practically equaling *A. scoparius* which had 17.7. The big bluestem, moreover, was found in a few more quadrats than the little bluestem, although both were of general occurrence in the type. Both species showed a wide variation in abundance, from 2 to about 40 per cent, but the amount of cover afforded by the little bluestem was more uniform and that of the big bluestem much more variable. This agrees with the general field studies, although it seems certain that over the area as a whole little bluestem is more important in the Stipa type than is the coarser and more mesic species.

Poa pratensis held the same place and almost the same ranking as in the little bluestem type, furnishing 5.1 per cent of the cover and occurring in 84 per cent of the quadrats. It was fairly uniform in amount, ranging between 1 and 15 per cent.

The forbs made up 2.4 per cent of the rather sparse basal cover and occurred in about three-fourths of the quadrats. *Sporobolus heterolepis* was

found in only 3 quadrats but at the rate of 10 to 15 per cent. Koeleria, which likewise constituted about 1.5 per cent of the cover, was more widely distributed and, except in one instance, never exceeded 2 per cent in any quadrat. Other grasses were of very little importance (Table 14).

TABLE 14. *Percentage of basal cover in Stipa spartea type composed of various grasses and forbs, and percentage of quadrats in which each occurred. First section, 25 quadrats in the upland Stipa type; second section, 7 quadrats in the lowland Stipa type; third section, same for 10 quadrats in the Sporobolus heterolepis type of uplands. All of the quadrats were taken from various prairies in the drier section of the general area.*

Species	Per cent cover	Per cent occurrence	Per cent cover	Per cent occurrence	Per cent cover	Per cent occurrence
Andropogon scoparius	17.7	84	0	0	11.1	60
Andropogon furcatus	17.5	96	19.1	100	11.6	90
Poa pratensis	5.1	84	6.8	100	3.7	70
Stipa spartea	51.2	100	67.0	100	1.1	30
Sporobolus heterolepis	1.4	12	.0	0	63.3	100
Sorghastrum nutans	.7	32	.1	14	1.4	30
Bouteloua curtipendula	.9	32	.7	43	1.2	50
Panicum scribnerianum, P. wilcoxianum	.2	20	.4	43	.1	20
Koeleria cristata	1.6	40	.1	14	.9	50
Elymus canadensis	.2	16	.0	0	.1	20
Panicum virgatum	.1	8	.1	14	.1	10
Forbs	2.4	72	3.8	100	3.1	60
Total	99.0	..	98.1	..	97.7	..

The outstanding facts revealed by these quadrats, aside from the abundance of Stipa and the low percentage of basal cover, are the great abundance of the bluestems and the importance of bluegrass. This may be stated negatively by emphasizing the relative unimportance of the other grasses which taken collectively afford only 5.1 per cent of the basal cover.

In a smaller number of representative quadrats on the lowlands of the dry area, the basal cover was 7.3 per cent and the percentage of Stipa 67. *Andropogon furcatus* entirely replaced the little bluestem and increased its former percentage to 19, being represented in every area. Poa, which was always present, constituted 6.8 per cent of the cover, and the forbs about 4. No other species made up even 1 per cent.

SPOROBOLUS HETEROLEPIS CONSOCIATION

Ten representative quadrats from 10 prairies in the Sporobolus type of the drier area gave an abundance of Sporobolus of 63 per cent and a total basal cover of 12.1. A maximum percentage for this dropseed was 98, thus showing its habit of sometimes growing in practically pure stands. Little bluestem was found in 6 of the quadrats and big bluestem in 9, each

furnishing approximately 11 per cent of the cover. Poa, found in about three-fourths of the areas, constituted 3.7 per cent which slightly exceeded

FIG. 45. Low prairie on "second bottom" along the Missouri River. The tall grasses form a dense foliage cover about 6 feet high and forbs are not abundant.
FIG. 46. Detail of *Andropogon scoparius* (right) and *A. furcatus* on June 15. The little bluestem is about 10 inches tall.

that of the forbs with 3.1 per cent. Stipa, Bouteloua, Sorghastrum, and Koeleria each constituted about 1 per cent and were found in half or less of the quadrats.

The importance of the forbs is often much greater than is indicated by these partial percentages of basal cover. Although large numbers of quadrats were selected at random, numerous others were made in areas chosen as typical of the general cover. Since major interest was centered in the percentage composition of the grasses, quadrats with an excessive development of forbs were usually avoided. In many prairies of both upland and lowland, forbs were never abundantly grouped; in others, especially where there was considerable surface erosion, they often constituted 10 to 15 per cent of the basal cover and only in the portions where the grasses were best developed did they fall as low as 5 per cent. The foliage cover was, of course, usually much greater. Big bluestem or other types of low-lying prairies that, because of drainage conditions, have become subject to periodic overflow usually experience a considerable increase in forbs (Fig. 5). It is in the least disturbed tracts that the dominants maintain the purest stand. Conversely, in grassland where mowing occurs two or more times during a single growing season, many species and especially those that are not confined to the ground layer may actually disappear. Both of these types of prairies were avoided in making these surveys.

RELATIVE GROWTH IN HEIGHT OF GRASSES

A large number of measurements was made in each prairie to determine the average height of the dominant grasses. The various prairies, especially in widely separated areas, were necessarily visited on different days and usually during different weeks. Hence the height growth of the grasses can not be compared on any given date. A study of the data shows, however, that the average height growth was much less in the areas of lower rainfall westward and northward, that it gradually increased in the central portion of the area, and was markedly greater in the best watered southeastern part.

In making comparisons of height growth, considerable variation was found not only in the individual prairie, due to local differences in water content and fertility of soil, but also in the same prairie from year to year, due to differences in seasonal precipitation. Hence, it seemed best to compare growth in a group of prairies in an area with that in other groups during the same season. Since *Andropogon scoparius* and *A. furcatus* are the most abundant and consistent species they were used to represent the behavior of the grasses in general (Fig. 46).

During 1929, the average height of *Andropogon scoparius* was found in a group of prairies in northeastern Kansas and southeastern Nebraska (Fig. 3). It was 13 to 18 inches high on July 12-13, and exceeded that at three stations near or northwest of Lincoln, studied on July 17-18, by 5 to 8 inches.

It was also taller by 5 to 7 inches than the average of three prairies in South Dakota and Minnesota (July 19-21).

On August 28-29 a series of stations from southeastern Nebraska eastward into Iowa showed an average height of this grass varying from 16 to 26 inches. This was 10 to 11 inches greater than in a similar group of grassland areas near Lincoln on July 29 to September 10.

The average height of *Andropogon furcatus* at three stations in southeastern Nebraska and northeastern Kansas, on July 9-12, was 22 to 28 inches. This exceeded by 9 to 12 inches the general level of the same species at three stations near or northwest of Lincoln, measured on July 17-19, as well as two in South Dakota and Minnesota visited on July 20-21. The height growth in three prairies in southeastern Nebraska and Iowa was 21 to 33 inches on August 28-30. This was 8 to 9 inches greater than at three others near Lincoln, July 25 to September 10.

During 1930 measurements of little bluestem were made at three stations in west-central Iowa on June 13-15. The average heights ranged between 8 and 18 inches. This was 2 to 8 inches greater than a similar group of prairies in northeastern Nebraska on August 1-3. During June 21-28 this grass averaged 10 to 15 inches tall at three stations near Lincoln but 18 to 22 inches at three others in northwestern Missouri. In five prairies in northeastern Kansas the average height range was 12 to 17 inches on July 17-20. This was 6 inches greater than at 4 stations in northwestern Iowa and one in southeastern South Dakota where the heights were measured a week later.

Measurements of big bluestem gave similar results. During June 27-29 the average heights of the foliage at 5 stations in northwestern Missouri were 21 to 33 inches. Only 3 to 6 days earlier measurements in three prairie areas near Lincoln ranged from 15 to 22 inches, i.e., 6 to 11 inches less. On August 18-19 three stations in northeastern Kansas gave a range in average heights of 16 to 30 inches. This was 2 to 10 inches greater than that at three others in northern Iowa, measured a week later.

During July 7-12, 1931, the little bluestem averaged 7 to 12 inches tall at a group of five stations in southern Nebraska and northern Kansas in the western border of the area. A week later measurement at five stations in west central Iowa showed averages which were twice as great. The big bluestem at this group of Iowa stations varied between 18 and 40 inches in average height on July 17-19. In four prairies somewhat west of Lincoln it was only 15 to 18 inches high one week later; and at four stations near the margin of the area southwestward 12 to 18 inches a few days earlier.

Along a line near and paralleling the Kansas border the rainfall decreases westward at an average rate of about an inch for every 25 miles. Conversely the evaporation rapidly increases. Traveling eastward along this line one observes a gradual increase in average height of the vegetation. Measure-

ments along a line from southern South Dakota southward through western Iowa into northwestern Missouri show a similar but more gradual increase in precipitation from 25 to 36 inches. This is accompanied by progressively earlier growth and an increase in length of the growing season southward, and results in greater stature of the prairie vegetation on equally fertile soil. The differences in height growth in the extreme types of grassland are indeed very striking.

The conditions more favorable to growth in the eastern and especially the southeastern part of the area are expressed not only by a greater growth in height but also in numerous other ways. Lowland grasses and sedges such as *Spartina michauxiana*, etc., extend much farther up the ravines, often indeed to the tops of the hills. *Carex festucacea*, for example, in the more xeric prairies is confined to low slopes or swales where it is usually only about 2 feet tall, but in the moister prairies it increases in stature to about 4 feet and is often abundant on the hilltops. The more mesic grasses, especially big bluestem and tall panic grass, extend their dominance farther up the slopes and there is a marked tendency towards the greater partial replacement of little bluestem except on the driest sites.

The more favorable growth is also shown in the greater density of stems within the sod or bunch. The clumps of little bluestem in the drier prairies of the north and west are frequently only one-third to one-half occupied by green stems; in the best situations southeastward 75 to 90 per cent of the area of the clumps is completely filled with stems. Still another indicator of relative drought is shown by the much greater tendency towards production of flower stalks in the southeast where they are well developed and abundant even on the driest uplands. This is in striking contrast to their small number and dwarfed appearance in the western prairies except during the wettest years.

Since the prairies near Lincoln were visited almost weekly and extended trips made weekly or fortnightly, excellent opportunity was afforded for repeated comparison of the relative development of the foliage cover. In general this decreased in any westerly direction and also to a smaller degree northward. This amounted in many cases to as much as 20 to 30 per cent. Southward, eastward, and especially southeastward even more significant increases were observed, ranging between 15 and 50 per cent, so that differences in the cover in prairies most distantly separated sometimes amounted to 60 to 80 per cent. These differences were found in prairies on both uplands and lowlands. In fact some of the upland prairies in southeastern Iowa and northern Missouri had a cover equaling or exceeding that of prairies on low ground westward from Lincoln.

These differences in foliage cover were repeatedly shown in the yields of hay. In the drier uplands this varied from 0.5-1 ton per acre as compared to 1.5 or slightly more in the more luxuriant vegetation southeastward. Big

bluestem lowlands in the southeast yielded 1.5 to over 2 tons per acre, a considerable increase over similar grasslands northwestward.

MINOR GRASSES AND GRASS-LIKE SPECIES

The grasses alone are the dominants of the prairie. Knowledge of their autecology, importance, and interrelationships is fundamental to an understanding of the prairie. Seven of the ten most abundant species of the prairie grasses characterize the grassland types just described. The importance of the other three species also has been briefly considered. For a complete account of their distribution and autecology the reader should consult "Ecology and Relative Importance of the Dominants of the Tall-Grass Prairie".

A brief account will now be given of other grasses and grass-like plants. Although the several types of grassland are mostly well defined, there is considerable mingling of the dominants over broad ecotones. Frequently a species such as big bluestem, which dominates extensive lowlands, is also found more or less regularly, although in diminished abundance, throughout upland types. This too is true of many minor species of grasses and sedges. Although further study will undoubtedly show considerable differences in regard to abundance and regularity of occurrence of the minor grasses in the various major types of grassland, yet owing to the large area investigated detailed investigations have in most cases not yet been made. Hence, the plants will be discussed under the broader divisions of those most common in upland types and those found more often in lowlands. Several species, such as *Poa pratensis*, range almost equally throughout.

SPECIES MORE CHARACTERISTIC OF DRIER GRASSLANDS

Bluegrass, *Poa pratensis* L., is a rather constant component of the prairie. It has spread very widely since the coming of the white settlers and is now found practically everywhere. It is an interesting example of the ecesis of an invader in a closed community. Several factors have contributed to the invasion of bluegrass along ravines and in lowlands and to its extension in smaller amounts into uplands. One of these is the general cessation of prairie fires. Burning appears to be more detrimental to Kentucky bluegrass than to any of the other prairie grasses. Although it practically always constitutes 1 to 3 per cent and often more of the basal cover over the region as a whole, yet in northeastern Kansas, for example, where a few farmers still follow the old practice of annually burning the prairies, bluegrass occurs very sparsely and may be entirely absent over large areas.

A second factor is that of the annual removal of the grasses by mowing for hay. Under natural conditions bluegrass can invade the tall-grass uplands only with difficulty and is kept out of the lowlands where the grasses are rank. The dense shade and the accumulated debris are great obstacles to the invader. It has been repeatedly observed that where the stand of big

bluestem and other grasses is dense, little or no bluegrass is found. In low ground, even where this grass was well established, protection from mowing or otherwise removing the tall grasses for a few years has resulted in its complete disappearance.

Bluegrass or June grass is a smooth perennial with numerous, long, running rootstocks arising from its base. The long, soft, flat leaf blades fold during drought. The height of the leafy, erect culms varies greatly, from 8 to 12 inches on dry uplands to 3 feet in lowlands where there is considerable shade.

In a large measure, its success as an invader is due to its vigorous early growth. It is the first grass to appear in spring. Often by the middle of February it has grown 1 to 2 inches on warm, south slopes. By the middle of April, when the bluestems are beginning to awaken, it has made a good growth. Very early in May the flower stalks begin to develop. During this month the pyramidal panicles, which are 2 to 4 inches long, appear. Blossoming takes place, seeds are formed, and much food is manufactured and stored in roots, rhizomes, and crowns before the new growth of native grasses (which were removed the preceding fall) seriously shade the invader. A survey of the prairies early in June reveals the panicles of the ripening bluegrass above or at the general level of the other grasses. During the hotter part of the summer it is less vigorous, often going into a semidormant condition until in early September, when it is revived by the autumnal rains. It then continues growth well into winter.

The great range of habitat is of interest. Bluegrass may occur on the driest ridges, where growth is usually scanty, increases in stature and often in abundance on the better watered slopes, and is regularly found under the big bluestem except where it is very dense. It thrives in the wetter areas dominated by *Panicum virgatum* and *Elymus canadensis,* for here the cover is always more open. It is usually found in areas of relict *Spartina michauxiana* and often with *Agrostis palustris* or *Tripsacum dactyloides,* although the shade is too dense for it where these grasses are best developed. Finally, it associates with relict *Eleocharis palustris* and various hydric sedges. This grass is the last species to disappear under the shade produced by large clumps of *Ceanothus pubescens, Silphium laciniatum,* etc. It thrives in disturbed areas as about gopher mounds, often growing up through 4 to 6 inches of deposited soil. In ravines it is prominent and is benefitted by flooding and deposition of sediment which greatly harm most species of the prairie. Along margins of scrub or forest it grows under a light intensity of only 10 to 12 per cent and becomes attenuated only when this is reduced to less than 8 to 9 per cent. Under grazing its invasion is greatly accelerated. It rapidly increases and under continuous close grazing finally takes almost complete possession.

Bluegrass was found to some extent in nearly every prairie. Its average

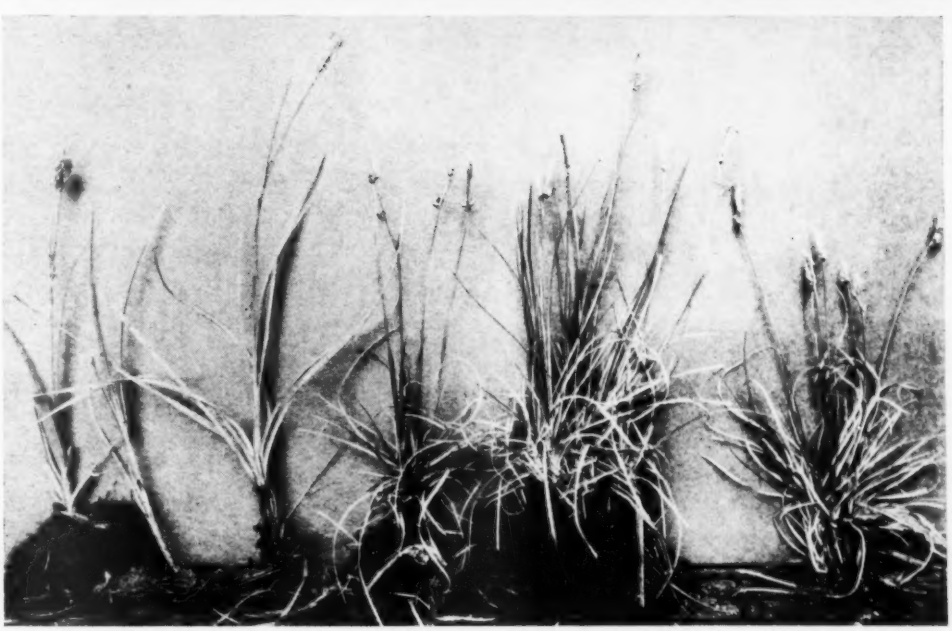

FIG. 47. Three species of interstitial grasses: *Panicum scribnerianum* about 10 inches tall (left), *P. wilcoxianum* (right), and *Poa pratensis* (center). Photo. June 11.

FIG. 48. Three plants of *Carex meadii* (left) and *Carex pennsylvanica* (right). Both species are in bloom. Photo. May 1.

abundance on uplands was 4.7 per cent of the basal cover, varying from 1 to 30 per cent. It may appear quite abundant and yet constitute only a very little of the plant cover. For example, in a typical upland quadrat where 197 tufts and 107 flower stalks were counted, it covered only 110 sq. cm. of the soil surface, i.e., occupied 1.1 per cent of the surface of the ground. These tufts varied from 0.1 to 2 cm. in diameter, 0.5 cm. being an average. In fact, on the dry uplands this grass is nearly always in small clumps which frequently have only 1 or 2 flower stalks but sometimes as many as 12 or more (Fig. 47). Bluegrass occurs between the tufts or bunches of the other grasses. On better watered slopes and lowlands the bunches are larger unless the shade is too dense. In ravines where mowing is frequent these bunches may form an almost continuous sod. On lowlands Poa constituted on an average about 9 per cent of the basal cover.

Panicum scribnerianum Nash is a low interstitial grass occurring almost everywhere in the prairie on both dry and moist soils. It is a small, erect perennial that propagates by means of short rhizomes. Growth is resumed early in spring, the broad leaves spreading in rosette-like clusters near the soil surface. The erect stems soon develop and the broad, short leaves (0.25 to 0.5 inch wide and 2 to 4 inches long) are carried upward into the light as the surrounding vegetation develops. In the uplands of drier sections a height exceeding 15 inches is unusual, but on low land where water is more plentiful and vegetation correspondingly more abundant, as well as southeastward on the uplands, the plants are often 18 to 22 inches tall (Fig. 47).

This species is best developed where the cover of vegetation is not too dense. Its ruderal tendencies are shown by its increased abundance in locally disturbed areas and especially where there is light grazing. It is not at all abundant and often does not occur where big bluestem and other tall grasses are well developed. The small tufts or bunches are usually only 1 to 4 inches in basal diameter and the number of stems varies mostly between 1 and 8; often there are about 3. The spread of the tops is frequently several times that of the base.

Flowering begins in late May or in early June. The first panicle is exserted and the large turgid spikelets are conspicuous. Later the stems may branch more or less dichotomously near the top. The basal leaves dry during midsummer and the widely spaced cauline ones produce neither much forage nor shade. Because of its wide distribution and consistent occurrence this grass ranks as one of the most important secondary species of grasses.

Panicum wilcoxianum Vasey is another panic grass of similar wide distribution and of only slightly less importance than the preceding, which it resembles in general habit. It is of somewhat smaller size (6 to 10 inches tall) than *P. scribnerianum* and can be rather readily distinguished from it by the shorter and narrower leaves, smaller panicles, and especially by its

much greater pubescence, which consists of long hairs (Fig. 47). Like the preceding grass, it grows in soil not already appropriated by the dominants, but blossoms somewhat later in summer. Advantage is taken of any disturbance such as mowing or burning which affords increased light, and the grass also increases greatly under moderate grazing. It is not commonly found in dense growths of the lowland grasses.

Panicum praecocius Hitchc. & Chase, distinguished by its habit of branching almost from the base and by the appearance of the secondary panicles before the maturity of the primary ones, is widely distributed but of much less frequent occurrence and also usually of less abundance than either of the preceding. Sometimes it forms a dense understory in wet, sandy soil to such species as *Agrostis palustris* and may also occur in the margins of sloughgrass alternes. But it is mostly confined to the drier types of grassland, where the slender, hairy culms reach a height of about 6 to 18 inches.

Other related species of relatively small importance are *Panicum perlongum* Nash and *P. huachucae* Ashe. They occur sparingly in some of the drier types of prairies.

The dropseed, *Sporobolus asper* (Michx.) Kunth, is frequently a constituent of prairie vegetation. This perennial, tufted, tall grass forms small clumps or occurs as scattered individuals in the sod matrix. In a few prairies it sometimes reached an abundance of 5 to 15 per cent; in others it fell to 1 to 3; but in many of the grasslands in the wetter part of the region it was not found. It increases greatly in abundance where there is disturbance and is very common on dry banks along roadsides, in many grazed prairies, as well as on dry, poorly vegetated ridges. It readily becomes semiruderal in habit as is shown along trails through the grassland and in recently broken prairie sod. The preference of this species for the drier uplands where vegetation is less dense and competition is not too severe is marked as is also its almost entire absence southeastward. During unusually dry summers it may appear to be quite abundant. Since it develops flower stalks and matures seed very late in the summer, annual mowing may have caused it to decrease in abundance (cf. Pound and Clements, 1900).

The erect, mostly unbranched stems reach a height of 1.5 to 4 feet. The narrow leaves are 1.5 to over 3 feet in length and are involute during drought. The upper leaf sheath more or less includes the strict compacted panicle which is 3 to 10 inches long (Fig. 44). Thus from late August until October the conspicuous inflorescence enables one to identify this grass even at some distance. The long leaves and stems, bleached white during winter and frayed by the wind, characterize the species during its dormancy. Growth is renewed with the bluestems, and even seedlings may form rather dense clumps and produce flower stalks the first year.

Sporobolus cryptandrus (Torr.) A. Gray, the sand dropseed, occurs much more infrequently than the preceding species, and then usually on sandy soil.

It was found, except as very scattered individuals, only in the drier prairies westward and was never of much importance. This species is similar to the preceding in stature, and is also a tufted perennial without rhizomes. It is easily distinguishable from *S. asper* by the spreading panicle which is 6 to 10 inches long and only the lower part of which is enclosed by the swollen sheath. The conspicuous tufts of hairs at the summits of the leaf sheaths are also characteristic.

Hairgrass (*Agrostis hyemalis* (Walt.) B. S. P.) is an interstitial species, found mostly on uplands but also on low ground. Although of very wide distribution yet it is of only minor importance. It occurs in small, isolated tufts, usually only 1 to 2 cm. in diameter but sometimes they are very much larger. Rarely are there more than 5 to 10 such tufts per sq. m. even where this grass is thickest in undisturbed prairie. The short, narrow leaves are tufted at the base; a few are scattered along the 6 to 15 or more slender erect stems. The species is noticeable only because of the large, widely spreading, purplish panicles with their whorled, scabrous branches. These appear early in June, usually above the general level of the grasses, and are 8 to 12 inches long. The foliage dries early and about the middle of June the panicles begin to mature. Later they break away from the plant and are blown far and wide, tumbling over the tops of the grasses as they are carried by the wind.

Eragrostis pectinacea (Michx.) Steud., purple Eragrostis, is a perennial of a somewhat weedy nature. It is found widely distributed over the prairies but rarely in abundance. The plant forms small, low tufts from the short, stout rootstocks and is conspicuous because of the handsome, open, purplish panicles, which mature after midsummer, separate from the plant, and tumble before the wind. Usually the panicles are few but sometimes as many as 35 to 45 stems occur in a single large clump. It is distinctly an interstitial species.

Certain sedges play a more or less important rôle among the grasses. Frequently they form 1 or 2 and sometimes, locally, 10 to 15 per cent or even more of the cover. In general they are more important in the drier and cooler parts of the region northward and westward where they are not so greatly overtopped by the grasses, and here also the number of species concerned is greater. The two most important species of uplands are *Carex pennsylvanica* and *C. meadii*, although *C. festucacea* is also commonly found on the uplands eastward.

Carex pennsylvanica Lam. is a low, rather leafy perennial that forms small tufts or bunches (Fig. 48). From propagation by rhizomes it sometimes produces areas of very open sod. Neither foliage nor flower stalks usually exceed a height of 12 inches; the leaves are often only 5 to 8 inches in height. This species ordinarily is a very minor component of the vegetation, but locally as on dry ridges, it may form 5 to 10 per cent over large

areas, and in very limited ones as much as one-third to one-half of the plant cover.

Where this sedge is at all abundant it produces a yellowish green ground cover late in March. The flower stalks are formed during April and soon the abundant orange-yellow stamens are shedding their pollen. The fruits ripen during late May or in June after which the whole plant is more or less obscured by the grasses. It is not easily mistaken for a grass, however, because of its pale yellowish green leaves as well as the dark underground parts.

Carex meadii Dewey is a much taller plant than the preceding with longer and broader leaves (Fig. 48). Typically it occurs in small tufts with only one or a few stems. It varies in height from 10 to 16 inches, the spikes considerably exceeding the foliage. Like the preceding, it starts very early before most of the grasses have broken their dormancy.

These sedges, with others, form abundant early grazing in the drier lands westward beyond the area of these studies. Mead's sedge is usually less important in our area than *C. pennsylvanica* since the plants are more widely scattered. It frequently occurs on more moist soil. Blossoming begins in April and flowers or fruits are conspicuous during May and June.

Carex festucacea Schkuhr. is a sedge of very wide distribution and of rather regular occurrence throughout the area. The stiff culms vary in height from 2 feet westward to nearly 4 in the moister climate eastward (Fig. 49). They usually exceed the height of the erect, rather stiff leaves, by at least one-third. The wand-like stems with their clusters of spikes are conspicuous above the grasses. The fescue sedge is very common in relict slough grass and in similar areas that are not too wet. Here it frequently constitutes more than half of the vegetation. This sedge occurs scatteringly over lower moist slopes and eastward it is also commonly intermixed in small amounts with the upland grasses, sometimes being common even on hilltops.

Juncus tenuis Willd. is found sparingly throughout the prairie in both dry and moist soil (Fig. 50a). In the drier sections of the prairie region it is largely confined to low ground or to prairie bordering lowlands. In the moister region it also occurs on upland, sometimes in considerable abundance. It is also found associated with *Carex vulpinoidea* and other hydrophytes, often in large amounts, thus showing a wide range of habitats. In the northern and western portions of the area, especially, it is not infrequent locally in draws in pure or nearly pure stands. On low land subject to overflow or very high water content in spring it frequently forms extensive alternes, constituting one-fourth to one-third of the vegetation (Fig. 42). In such places it is usually only 9 to 15 inches tall by midsummer; eastward it may reach twice this height.

This slender rush is perennial. The plants occur in small tufts which are 2 to 4 inches in diameter. The clusters of narrow leaves, which are

often involute during drought, extend to only one-third or one-half the height of the much elongated, leafless stems. The latter may occur singly or in small numbers but often 40 to 50 arise from a single clump. These develop the apparently terminal inflorescence, which is exceeded by its lowest leaf, late in June. The virgate stem and flower clusters make the species conspicuous even where the individuals are few.

The tall nut-rush, *Scleria triglomerata* Michx., is a constituent of some importance in many areas of the prairies, especially in the better watered portions of the grassland. It is distributed over a wide territory and sometimes constitutes locally 30 or even 50 per cent of the vegetation, as at the heads of draws. This leafy sedge was found in no great abundance except in a few locations and was almost or entirely lacking in most of the prairies in the drier half of the area. It arises from stout, clustered rootstocks. The 3-angled stems reach a height of 1.5 to 3 feet and the prominent, terminal flower clusters with their smooth, bony, white achenes are conspicuous by midsummer since they usually stand well above the grasses.

The wheat grasses are of very minor importance as constituents of the various types of grassland in the general area. *Agropyron smithii* Rydb. may be found abundantly along roadsides almost anywhere. It frequently forms a dense, almost exclusive sod with the foliage 2 feet high and the abundant

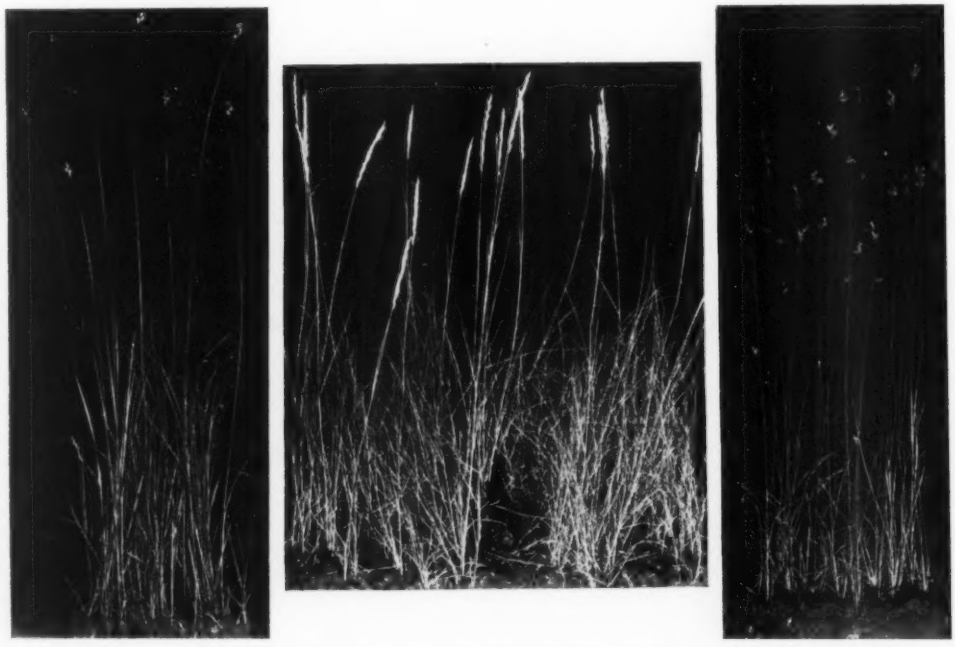

FIG. 49. Sod of *Carex festucacea* (left) on July 5, the flowers are borne at a height of about 3.5 feet.

FIG. 50. Open sod of *Agropyron pseudorepens* in poorly drained lowland near Clay Center, Nebr., on July 10. Note the absence of other species and the large cracks in the soil.

FIG. 50a. *Juncus tenuis* (right) about 2 feet high. Photo. July 5.

flower stalks reaching a level of about 3 feet. But in the prairie proper it rarely occurs except where there has been some disturbance. An old road or a series of parallel roads through a large tract of prairie may be bordered with this sod-forming species. It thrives in hard, compacted soil. Careful study shows conclusively that it can not invade the undisturbed prairie, and eventually it loses the territory in its possession when the disturbance is removed. The small sprinkling of this grass that is sometimes found here and there in the prairie may be explained on the basis of a slight disturbance. On the uplands it was found on the drier, western border of the area in thin stands but only locally on the driest slopes. This indicated the proximity of the great mixed prairie region where the wheat grasses are important dominants. This grass is of boreal origin which accounts for its very early growth in spring.

Agropyron pseudorepens Scribn. & Smith and *A. smithii* (to a lesser extent) are also found on low ground. They frequently border alkali flats where they are of considerable importance. In the western half of the area especially, great tracts of low, poorly drained soil are characterized by a pure or nearly pure growth of Agropyron. Such soils are usually wet and in spring often poorly aerated, compact, and of high clay content. They form cracks upon drying in summer and are an unfit place for most prairie grasses (Fig. 50). Here are found thin or moderately thick stands of wheat grass, often dwarfed in size and far below normal in number and size of flower stalks. The basal cover usually varies from 2 to 15 per cent. Much of the soil is bare. By midsummer the grass may dry except a few of the upper, younger leaves and leaf sheaths which remain green. The flower stalks are often as few as 75 to 150 per sq. m. The general level of the foliage is only 9 to 15 inches and that of the flower stalks 20 to 26 inches. Only where conditions are unusually favorable to growth or where wheat grass intergrades into the sod of tall panic grass or big bluestem is the stand denser and the plants better developed. Wheat grasses are almost invariably found, either in mixtures with other species or in pure growth, in the transition from areas of salt grass *(Distichlis spicata)* to low prairie. They are frequent in native pastures, especially where much trampling has occurred.

The blue grama (*Bouteloua gracilis* (H. B. K.) Lag.) is a tufted, perennial, sod-forming short grass that is characteristic of the Great Plains and mixed prairies westward where it is a dominant. It is also sometimes found on the thin soils on the brows of the steeper hills, especially the xeroclines, occasionally on much eroded, steep slopes bordering ravines, and in similar places in the drier parts of the region under study. Here it may occur only as scattered tufts or it may dominate local areas. Its increasing abundance in the understory in undisturbed grassland is an indication of the proximity of the mixed prairie. It flourishes in the more humid climate eastward and, as has been shown experimentally, increases in proportion to

the degree that the taller grasses are handicapped by frequent mowing or grazing (Clements, Weaver, and Hanson, 1929). Where overgrazing has occurred the whole area may consist of mats of grama grass and other short grasses.

The numerous short leaves appear early in April but reach a general level of only 3 to 5 inches by midsummer. The flower stalks are about 8 to 12 inches high and have 2 or 3 spikes approximately an inch long. The spikes, both terminal and lateral, turn with the wind like weather vanes.

The aggressiveness and persistence of this species, where not too much shaded, is due in part to its rapid growth and excellent root system. The latter is very fine, deep, and minutely branched. Seedlings 6 weeks old may have a primary root 10 inches long. With the production of tillers at this time, the secondary root system appears and soon extends into the moist soil below the surface. By midsummer the grass forms a dense sod and by autumn the widely spreading roots extend well into the second foot and some into the third. Mature plants have a root system which descends 5 or more feet. Usually seed production does not occur the first year. Over most of the region the tall-grass cover is too dense for the growth of this western invader which with other short grasses is a relict of a former dry phase during which the mixed prairie moved eastward in consequence of a pronounced climatic change.

The black grama (*Boutcloua hirsuta* Lag.) is found in situations similar to those where blue grama occurs, especially if the soil is rocky or contains gravel or much sand. Actually it is much less abundant. The two species are similar in life form and habitat requirements. Owing to their dwarf form and original home on the high foothills and plateaus of the southwest, they easily withstand the drought of the most xeric places of the tall-grass region where they do not belong climatically but are relicts of a drier climatic phase.

The buffalo grass (*Bulbilis dactyloides* (Nutt.) Raf.) is another dominant short grass of the Great Plains that occurs in small amounts along the western border of this area. This low, stoloniferous perennial has short leaf blades which, like those of the grama grasses, roll tightly during drought. The plants are unisexual and since propagation is largely by stolons and short rhizomes, small isolated sod mats often consist entirely of plants bearing either staminate or pistillate flowers. The staminate spikes occur in groups of 2 or 3 on slender erect culms usually only 4 to 6 inches high. The culms bearing the pistillate spikes or heads are so short that the inflorescence is partly hidden among the leaves. The seedlings are monoecious (cf. Hitchcock, 1920).

This species requires more water than the short grama grasses and is found sparingly in draws where it sometimes forms pure dense mats of limited extent. More usually it is associated with *Bouteloua gracilis* on the thinner soils of the uplands. Where pure, it forms a close, soft, grayish green

turf. The root habit resembles that of the shorter Bouteloua both in fineness and degree of branching as well as in rapid development. It often penetrates even more deeply. Short stolons develop the first year of growth and they are 3 to 10 inches in extent by June of the second summer. It forms a denser sod than the grama grasses but like them is almost or entirely shaded out by the taller competitors. Altho often abundant in overgrazed pastures throughout the drier half of the area, in competition with the undisturbed tall grasses it is of only very minor importance even on the western border of the region under consideration. Wherever this species occurs certain forbs are almost invariably associated with it, especially *Hedeoma hispida, Plantago purshii,* and the low annual grass, *Festuca octoflora.*

A few of the fescue grasses are to be found mostly on the thinner, poorer soil, especially throughout the drier parts of the prairie. Chief among these are the slender fescue grass (*Festuca octoflora* Walt.) and sheep's fescue (*F. ovina* L.). These are low, tufted grasses with involute or setaceous leaves and occur as interstitials between the clumps of the dominants. They are rarely abundant except very locally on dry slopes or gravelly ridges, or similar xeric habitats. They are conspicuous only when the panicles develop. The heights of the plants vary greatly, from 3 to about 14 inches, depending upon the seasonal rainfall and the degree of competition. They are practically always of minor importance.

A few species of Muhlenbergia, of which the perennial *M. racemosa* (Michx.) B.S.P. and *M. mexicana* (L.) Trin. are the most important, are frequently found along the margins of grasslands, as components of slightly disturbed vegetation of ravines, or in other disturbed areas in the prairie. They are best developed where the soil is continuously moist and they sometimes frequent the margins of swampy land. They are nearly always of minor importance.

Calamovilfa longifolia (Hook.) Hack., the sand reed, is a coarse, tall grass with extensive rhizomes. It was found along the Platte River and in a few other places but always on loose, sandy soil. This indicator of a sandy substratum has migrated eastward from its stronghold in the great sandhills region westward but is of small importance in the area under study.

A small amount of wire grass (*Aristida longiseta* Steud.) occurs in the uplands of the extreme northern and western portions of the area, especially on very light types of soil. It was usually very thinly distributed but in a few sandy soils it composed locally as much as 30 per cent of the vegetation. *Stipa comata* Trin. & Rupr. may occur in similar situations.

Elymus macounii Vasey is a species of wild rye that is found but rarely except in the northern third of the region where it is of rather frequent occurrence. Here it is conspicuous since the isolated or loosely aggregated stalks stand far above the general level of the vegetation. Ecologically it is of little importance.

The preceding grasses and sedges by no means exhaust the list of such species that are to be found in the prairie. It is of interest to note, however, that with few exceptions, even these are of minor importance when compared with the seven major dominants found in well drained soils. Numerous other species occur, but further detail would merely obscure the more significant ecological relations.

SPECIES MORE CHARACTERISTIC OF WETTER GRASSLANDS

Many hydric grasses and sedges are intermixed with *Spartina michauxiana* or form alternes with it. These are also found more or less regularly in the moister portions of the Panicum-Elymus transition, and frequently recur also in the wetter parts of the general areas dominated by *Andropogon furcatus*.

Tripsacum dactyloides L. occurs only in the southeastern part of the area; a northern outlier was observed at Union, Nebraska, due east of Lincoln, near the Missouri River. This coarse, robust perennial is found not only in transitional areas between big bluestem and slough grass, but also often occurs in small clumps or as isolated plants on springy hillsides. It is distinctly a bunch former, the very coarse, scaly rhizomes often being partially exposed on the soil surface. The more or less circular bunches vary from 12 to more than 40 inches in diameter (Fig. 51). The older ones are often bare in the middle except for a sprinkling of bluegrass, but usually 10 to 20 coarse stems are produced per square decimeter. These are quite woody, somewhat

FIG. 51. Isolated clump of *Tripsacum dactyloides* about 5 feet high and in full bloom. Union, Nebr., June 24.

FIG. 52. Characteristic clump of *Agrostis palustris*, July 12. It is about 3.5 feet tall and in blossom.

flattened, 1 to 7 feet in length, and 5 to 10 mm. in greatest diameter. There are 7 to 10 coarse leaves 1 to 3 feet in length and 0.5 to 1.3 inches in width. The dense foliage often reaches a general level of about 44 inches and spreads so widely that the basal area is less than half that of the tops. The shade is so deep that there usually occurs little else than bluegrass where the stand is at all dense. The flower stalks reach heights of 5 to 8 feet. The conspicuous inflorescences are 8 to 10 inches long and both terminal and axillary. There are usually 3 to 5 flower stalks from a single stem. The terminal spikes are mostly in threes; the axillary ones usually solitary. Flowering begins late in June; when completed, the terminal staminate portion of the inflorescence is shed. Later the pistillate part below breaks up into bony, seedlike joints. Where at all abundant, gama grass furnishes good forage and when cut for hay the yield is heavy. Usually two or three cuttings are made each growing season; sometimes a single cutting yields 3 tons per acre.

Red top (*Agrostis palustris* Huds.) is an erect, sod-forming grass 2 to 4 feet tall, often with a decumbent base, and vigorous rhizomes 2 to 6 inches long (Fig. 52). It thrives in wet soil where competition with big bluestem and other grasses is not severe and it also grows in depressions covered with water during spring and early summer. Thus in nearly level bottom lands, islands of red top often mark the depressions. This grass is frequently found as isolated clumps; it forms more or less pure alternes with Spartina, *Panicum virgatum*, and various sedges; or intermingles as an understory 2.5 to 3 feet high to these tall, wet land species, especially along their margins. In the moist soils it forms all degrees of mixtures with *Andropogon furcatus*. Numerous dense, fairly pure stands occur locally, and it frequently forms 80 per cent of the grass mixture. In the prairies southeastward it sometimes advances up the lower slopes. The rather short, flat-bladed leaves do not cast a dense shade. Often the lower leaves are dead to a height of 6 inches and the general leafy level seldom exceeds 12 to 18 inches. Hence, an understory of bluegrass is often present even in the densest areas of Agrostis. The large, widely spreading panicles, 2 to 12 inches long, and usually reddish in color, give this species its common name. Blossoming occurs during midsummer. Although this species is of wide distribution, extending throughout the region, it is of relatively minor importance.

Reed canary grass, *Phalaris arundinacea* L., is a coarse perennial that frequently occurs in moist soils and wet areas too poorly aerated for most other grasses. Like most species of lowlands, where competition for light is severe, this species resumes growth early, usually late in March. Early in May the coarse stems are a foot or more in height and in the fifth or sixth leaf stage. Owing to rhizomes, which spread widely, it forms dense stands, often 15 to 20 stems per square decimeter. Hence, in July when the foliage is 2.5 to 3.5 feet high the shade is dense. In fact, the lower leaves are often

dead to a height of 6 to 12 inches. The flat leaf blades of this coarse, rank grass are often nearly half an inch wide. The stems are usually 3.5 to more than 5 feet tall (Fig. 53). Blossoming occurs in the loose spike-like panicles from June to August. Westward and northward, owing to a deficient water supply, the plants are of much smaller stature.

Elymus jejunus (Ramaley) Rydb., western wild rye, is of rather frequent occurrence in low prairies of a wetter type than those occupied by big bluestem. It is 2 to 3 feet high and is sometimes found as an understory in open stands of slough grass or tall panic grass, or associated on more or less equal terms as regards height with *Carex vulpinoidea* and other sedges. Frequently it demarks poorer types of soil. It rarely occurs even in limited pure stands and is nearly always of distinctly secondary importance. Heading and blossoming occur in June and July.

Torrey's rush, *Juncus torreyi* Coville, is found usually sparingly but sometimes in considerable local abundance in areas dominated by Spartina, and in other types of grassland common to wet soil. It is also found in the sedge meadows and similar hydric places. The conspicuous inflorescence of many heads is characteristic as are also the tuber-like thickenings on the slender rootstock of this rather tall perennial (Fig. 54).

In marshy areas that are not occupied by slough grass, the creeping spike rush, *Eleocharis palustris* (L.) R. & S., frequently abounds. This species

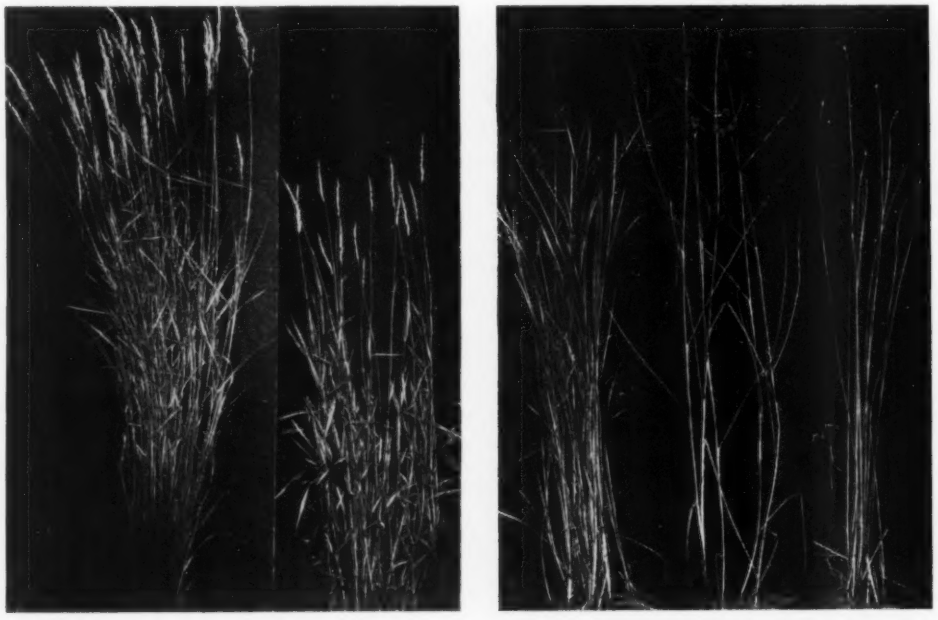

Fig. 53. *Phalaris arundinacea* (right) 3.5 feet high with ripe fruits on June 24, and *Calamagrostis canadensis* 4.5 feet tall on July 12. Both are species of low, wet ground.

Fig. 54. *Carex vulpinoidea* (left), *Juncus torreyi* (nearly 4 feet tall), and *Scirpus americanus*. All are species of wet meadows. Photo. July 12.

is perennial by horizontal rootstocks, the annual crop of terete stems forming much debris. It varies in height from about 8 to 10 inches in the broad swales in the drier parts of the area to 16 to 18 inches or more along the first bottoms of the Missouri. The sod is not so dense where the water supply is variable. This species is abundant in spring and early summer over many acres of low, poorly drained lands from Dakota through Nebraska and Iowa to Kansas. In this region the spike rushes (including especially the much smaller *E. acicularis* (L.) R. & S.) form great alternes or frequently an understory in the more open stands of low slough grass or in the open growth of wheat grass in the swales. Either as small islands in the lowest ground or as an interrupted understory in the most mesic grasses, they are found in many low prairies throughout the entire area. Like most plants of lowlands they renew growth early, especially where there is an abundance of water and not too much debris. Normally they are several inches high early in April and by the middle of May the spikes are developing. This is followed by blossoming in June and July. Few other species are associated with Eleocharis where it is dominant.

The rather tall, wood reed grass (*Cinna arundinacea* L.) occurs sparingly in areas of lowland vegetation more hydric than the big bluestem.

Two species of rice grasses, *Leersia oryzoides* Poll. and *L. virginica* Willd., both with creeping rootstocks, are found in wet areas. In a few places only did they occur in any considerable abundance, usually they are only an occasional component of the wettest types of grassland and often occur more abundantly in the reed-swamp stage of the hydrosere.

Bechmannia erucaeformis (L.) Host (*B. syzigachne* (Steud.) Fern.) is found in wet places, especially along the larger river courses, but usually very sparingly. It is never of much importance except locally.

Calamagrostis inexpansa A. Gray and *C. canadensis* (Michx.) Beauv. are frequent in wet areas along the Platte River and in other low or swampy grounds. They were not found in very great abundance (Fig. 53).

Panicularia (*Glyceria*) *nervata* (Willd.) Kuntze, manna grass, is not uncommon in wet areas especially in the transition from the big bluestem to wetter grassland types. Usually it composes but a small percentage of the vegetation, but in certain small areas it may constitute half or more of the plant cover.

Sphenopholis obtusata (Michx.) Scribn. is a rather widely distributed species in the prairies but rarely occurs in any considerable abundance. Only in a few places was it found to constitute as much as 1 to 5 per cent of the vegetation.

Among the many sedges of wet areas the fox sedge, *Carex vulpinoidea* Michx., is one of great abundance and wide distribution (Fig. 54). In hundreds of places that are too wet for grasses it forms alternes, often of great extent, the roots forming a dense network in the muddy soil. Sometimes such

alternes constitute one-third to one-half of the vegetation. Here it frequently reaches a height of 2 to over 3 feet and occurs in dense stands forming nearly a pure sod-like growth. The extensive rhizomes produce 5 to 20 stems per square decimeter. Although the foliage cover is usually 100 per cent, actually the nearly leafless stem bases occupy only 3 to 12 per cent of the soil surface. Where less dense, a thin stand of *Poa pratensis* often occurs. Forbs are usually not abundant because of the dense shade; frequently the old debris is 5 to 7 inches deep. But where the area becomes drier numerous species such as *Steironema ciliatum* and *Asclepias sullivantii* are found.

In many lowlands, this carex is found scatteringly as a 1 to 15 per cent mixture in the low prairie. It indicates by its denser grouping the places of higher, local water content. Other areas are shared with Spartina or even with relict Phragmites. It is rather regularly found in all draws that are sufficiently wet either as isolated patches or intermingled with other species of the swamp. Thus it may occur on fairly high ground.

This perennial carex renews growth very early. Late in March it is often 4 to 7 inches tall. The slender, three-angled culms with their numerous leaves attain full height of 3 to 3.5 feet and fruit abundantly late in June. The numerous spikes with their dull brown to greenish color form a somewhat interrupted, narrow head usually 2 to 3 inches long. These are very conspicuous. This sedge was found in low ground adjacent to prairies in all of the six states visited.

Carex hystricina Muhl. is another sedge with a wide distribution but of somewhat less importance. This perennial appears early in spring and is often 4 to 6 inches high before the slough grass has produced its first leaves. It sometimes occupies land wetter than that in which slough grass grows, but may form dense alternes with it, almost in pure stands or accompanied by *Persicaria muhlenbergii* and other marshy forbs. By the end of May this slender, erect sedge has developed all of its broad leaves and soon the spikes are formed in abundance.

Among a few of the other most common and important marsh carices is *C. longirostris* Torr., which frequently constitutes a considerable part of marsh land hay. *C. davisii* Schw. & Torr. is frequent in bottom lands as is also *Fimbristylis interior* Britton.

Salt grass (*Distichlis spicata* (L.) Greene, *D. stricta* (Torr.) Rydb.) occasionally occurs in shallow basins but it is not frequent except on the margins of more extensive alkali areas (Fig. 55). It is a good indicator of a moderate degree of salt, being one of the most alkali-enduring grasses. It nearly always grows on soil with a shallow water table. Distichlis is a perennial, sod-forming grass that spreads by means of vigorous rhizomes. The harsh, salty leaves rarely exceed 8 to 10 inches in height but are exceeded by the flower stalks; the pistillate and staminate flowers are borne separately on different plants. When grazed it forms a dense sod and affords

the best forage under close grazing. It is sometimes accompanied by small amounts of alkali saccaton or tussock grass, *Sporobolus airoides* Torr.

In conclusion it may be stated that of the 20 grasses and 5 sedges and rushes enumerated as generally more abundant on uplands, only a few approach in ecological importance any of the ten grasses selected for detailed descriptions (Weaver and Fitzpatrick, 1932). Among these *Poa pratensis*, which is also widely spread on lowlands, ranks highest. *Panicum scribnerianum* and *P. wilcoxianum* also hold a high rating. *Sporobolus asper* and *Carex pennsylvanica* are other species of considerable ecological significance. The others are either widely spread interstitials or are of only such local importance as to be of less ecological significance over the area as a whole.

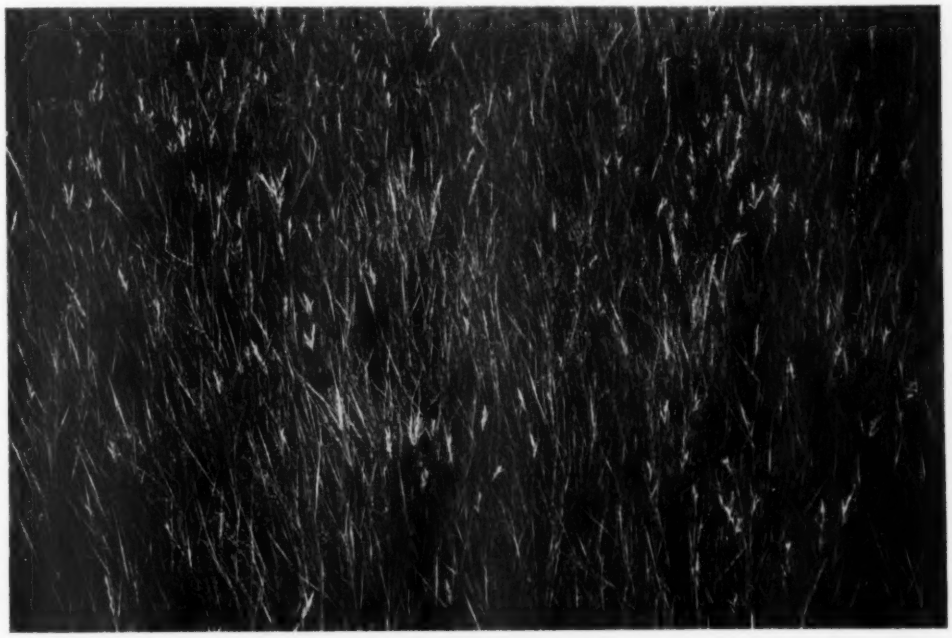

FIG. 55. Characteristic sod of *Distichlis spicata*. The grass is 6 to 8 inches high and in blossom.

Among the 22 species of lowlands, *Poa pratensis*, *Agrostis palustris*, *Carex vulpinoidea*, *Tripsacum dactyloides*, and *Eleocharis palustris* are the most important. All of the other species mentioned are of some importance in the structure of the vegetation but in comparison with the rôle played by *Spartina michauxiana*, *Panicum virgatum*, or *Andropogon furcatus* they are of minor significance.

RELATIVE IMPORTANCE AND DISTRIBUTION OF FORBS

Forbs are always components of the prairie. Often they are more conspicuous, although nearly always of less importance, than the grasses (Fig. 56). There are approximately 142 species of forbs that are of sufficient im-

portance, when considering the structure of the grasslands, to warrant more or less careful study. These fall rather naturally into two groups of nearly equal size, those that are more important in high prairies and those of greater ecological significance in the lowlands. These include all those species that were found in at least 10 per cent of the 100 upland or 35 lowland areas studied.

SPECIES MORE CHARACTERISTIC OF UPLANDS

A group of 75 of the most important species of uplands is given in Table 15. The species are arranged in the order of their importance as determined by their percentage of occurrence as societies of the first and second class. Thus *Amorpha canescens*, which was absent from only 7 per cent of the upland areas, ranked as a society of the first class in 74 per cent of these and as a society of the second class in 6 per cent.

TABLE 15. *Distribution and relative importance of the chief forbs of upland prairie and their occurrence in lowland. The numbers under columns 1, 2, 3, etc., give their percentage occurrence as a society of the first, second, etc., class, and the numbers under column 0 the per cent of prairies in which the species did not occur.*

Species	High Prairie						Low Prairie					
	1	2	3	4	5	0	1	2	3	4	5	0
Amorpha canescens	74	6	7	4	2	7	9	0	9	25	9	48
Helianthus rigidus	66	7	7	4	3	13	19	5	14	11	0	51
Aster multiflorus	44	15	21	5	0	15	25	3	22	14	11	25
Antennaria campestris	39	20	13	4	2	22	8	6	11	11	8	56
Erigeron ramosus	47	11	18	6	3	15	15	15	10	17	15	28
Solidago glaberrima	32	12	20	12	0	24	9	6	9	17	3	56
Psoralea argophylla	37	6	13	10	8	26	8	3	8	10	14	57
Petalostemon candidus and P. purpureus	22	17	13	20	2	26	4	2	4	18	6	66
Echinacea pallida	20	8	12	18	8	34	0	0	6	9	9	76
Euphorbia corollata	20	5	8	4	3	60	8	0	3	8	16	65
Solidago rigida	16	8	24	20	6	26	6	3	17	14	17	43
Astragalus crassicarpus	10	13	13	12	9	43	0	0	0	0	9	91
Liatris scariosa	14	8	17	16	7	38	3	0	3	5	5	84
Rosa arkansana	13	8	27	26	0	26	18	18	5	16	8	35
Coreopsis palmata	15	6	3	2	1	73	0	0	0	0	0	100
Kuhnia glutinosa	16	3	18	28	13	22	0	11	3	5	11	70
Psoralea floribunda	17	2	3	7	9	62	0	0	3	0	3	94
Sisyrinchium angustifolium and S. campestre	4	12	24	11	0	49	4	4	7	3	4	78
Ceanothus pubescens	8	8	8	8	8	60	0	0	0	0	0	100
Liatris punctata	10	5	18	16	9	42	0	0	0	0	2	98
Meibomia canadensis and M. illinoensis	8	7	14	24	5	42	18	7	16	5	11	43
Aster laevis	4	9	4	6	1	76	0	0	3	6	0	91
Artemisia gnaphalodes	6	6	24	25	9	30	5	5	18	18	10	44
Lespedeza capitata	5	6	17	17	10	45	0	9	17	17	11	46
Morongia uncinata	7	2	1	2	3	85	0	3	0	0	0	97
Solidago rigidiuscula	4	4	12	19	9	52	3	0	3	3	3	88
Aster azureus and A. sagittifolius	5	1	1	2	4	87	0	0	0	6	0	94
Linum sulcatum	1	4	24	18	7	46	3	0	5	5	3	84
Achillea occidentalis	4	1	11	15	20	49	3	0	10	12	15	60
Senecio plattensis	2	3	10	4	7	74	0	3	9	3	0	85
Baptisia leucantha	5	0	7	13	9	66	0	3	3	3	14	77
Baptisia leucophaea	2	2	15	21	6	54	0	0	0	6	14	80
Salvia pitcheri	1	3	5	5	11	75	0	0	0	8	6	86

TABLE 15. *(Continued)*

Species	High Prairie						Low Prairie					
	1	2	3	4	5	0	1	2	3	4	5	0
Lepachys columnaris	1	3	3	19	6	68	3	3	5	13	5	71
Pedicularis canadensis	2	2	1	6	2	87	0	3	0	0	0	97
Salix humilis	2	2	1	3	0	92	0	0	0	0	0	100
Anemone cylindrica	1	2	13	6	18	60	10	0	7	2	2	79
Comandra umbellata	2	1	8	16	7	66	3	3	8	3	3	80
Liatris squarrosa	3	0	8	4	2	83	0	0	0	0	0	100
Ruellia ciliosa	2	1	8	2	3	84	0	3	3	3	0	91
Viola pedatifida	0	2	8	12	11	67	0	0	5	3	3	89
Euthamia graminifolia and E. nuttallii	2	0	5	7	7	79	0	0	0	0	3	97
Plantago purshii	0	2	4	1	3	90	0	0	0	0	6	94
Lygodesmia juncea	0	2	3	5	4	86	0	0	0	0	3	97
Solidago mollis	1	1	3	5	2	88	0	1	0	1	1	97
Oxytropis lambertii	1	1	2	4	3	89	0	0	0	0	0	100
Eryngium yuccifolium	0	1	7	6	5	81	3	0	5	3	0	89
Polygala alba and P. viridescens	0	1	5	2	3	89	0	0	6	0	3	91
Pedicularis lanceolata	0	1	4	0	2	93	0	3	0	3	0	94
Callirrhoe alcaeoides	1	0	2	3	3	91	0	0	0	3	0	97
Drymocallis agrimonioides	0	1	1	10	15	73	0	0	0	0	0	100
Physalis lanceolata	0	1	0	14	23	62	3	0	0	11	17	69
Lithospermum linearifolium	1	0	0	10	24	65	0	0	0	16	14	70
Onosmodium occidentale	1	0	0	2	12	85	0	0	0	0	3	97
Psoralea esculenta	0	0	9	21	21	49	0	0	0	0	3	97
Hedeoma hispida	0	0	7	10	10	73	0	0	2	0	9	89
Hieracium longipilum	0	0	6	14	17	63	3	0	0	0	12	85
Aster sericeus	0	0	4	16	23	57	0	0	0	0	3	97
Delphinium virescens	0	0	4	10	22	64	0	0	3	9	20	68
Meriolix serrulata	0	0	3	11	11	75	0	0	0	0	6	94
Lithospermum canescens and L. gmelini	0	0	3	9	7	81	0	0	3	0	6	91
Asclepias tuberosa	0	0	1	11	23	65	0	0	0	11	19	70
Gentiana puberula	0	0	1	7	31	61	0	0	0	0	7	93
Specularia perfoliata	0	0	1	2	9	88	0	0	0	3	3	94
Acerates floridana	0	0	0	7	15	78	0	0	0	0	5	95
Allium mutabile	0	0	0	5	10	85	0	0	1	1	3	95
Acerates viridiflora	0	0	0	1	14	85	0	0	0	0	9	91
Allionia linearis	0	0	0	2	5	93	0	0	0	0	6	94
Acerates angustifolia	0	0	0	1	9	90	0	0	0	0	3	97

The ecology of the seven upland forbs of greatest importance is given first, after which the remaining species that are described are, for convenience of reference, arranged alphabetically by genera.

AMORPHA CANESCENS

Amorpha canescens Pursh, a half-shrub,[7] is perhaps the most conspicuous and characteristic subdominant of upland, tall-grass prairie. On a very large number of the prairies it formed the most important and most extensive societies (Fig. 57). The seedlings, which are often abundant, are very tolerant of shade but develop slowly where competition is great. Old plants renew growth about May 1 when the buds open on old stems if the area has not been mowed. Under the practice of annual mowing the woody top is

[7] A few half-shrubs and shrubs, viz.: *Amorpha canescens, Rosa arkansana, Ceanothus pubescens, Salix humilis,* and *Rhus rydbergii* are, for convenience, included with the forbs. Their rôle in the grassland where mowed each autumn is essentially that of forbs.

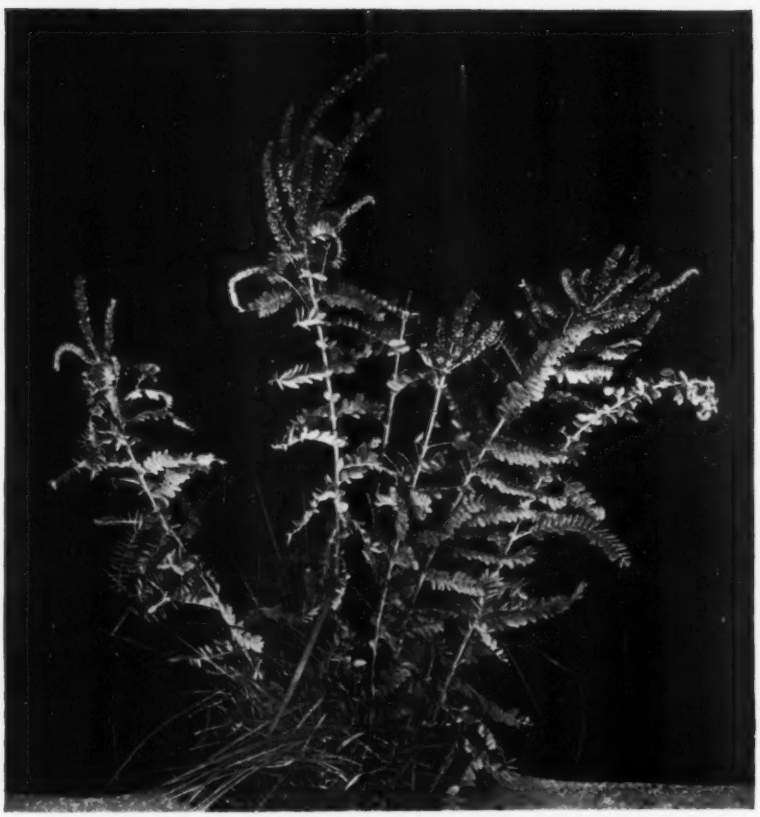

Fig. 56. Prairie near Crete, Nebr., on June 25, showing an abundance of forbs; *Erigeron ramosus* is most conspicuous.

Fig. 57. *Amorpha canescens* in blossom on June 30 at a height of about 15 inches. Aside from the grasses this is the most important species of uplands.

removed each year and the plants produce 2 to 5 or more basal stems. Plants frequently occur at the rate of 12 to over 20 per square meter but the number of stems may average two to three times as great. In areas where it is thickest, usually on the lighter, poorer types of upland soil, a maximum of 50 to 60 plants has been found per square meter. In fact in limited areas they even exceed the grasses in importance. Early in June, if the plants are at all abundant, they give to the landscape a leaden colored tone. By the latter part of June, when flowering begins, the plants are 12 to 20 inches tall and later they sometimes reach a height of more than 3 feet. They usually do not stand erect but lean outward at various angles.

The dark purple or indigo flowers are conspicuous for several weeks. The clustered terminal flower stalks occupy the upper one-fourth to one-third of the stem. There are usually 12 to 24 spike-like racemes in a cluster at the top of the stem. Each spike, which is 2 to 6 inches long, is crowded with dozens or even scores of tiny violet or purple flowers, so that the total inflorescence is very conspicuous. The flower contains a single petal, the standard, which is wrapped around the stamens and style. Hence the name Amorpha which is Greek for deformed.

Mature plants vary from 16 to more than 38 inches in height, depending upon the water supply and amount of shade, and until late summer conspicuously overtop the upland grasses. The large, compound leaves are abundant. They vary from 2.5 to 7 inches in length and occur at an average rate of 2 or 3 per inch of stem. They are about 1.2 to 3 inches in width. Where the societies are best developed, the cover of grasses is always reduced, sometimes as much as 30 per cent, as may clearly be demonstrated by removing Amorpha. During late July and August, especially if water is not abundant, the stems may become defoliated, by the natural dropping of the lower leaflets, to a height of 6 to 9 inches. In the dense shade of low prairie species, defoliation may extend somewhat higher. The remainder of the leaves, however, remain green until frost. Where mowing does not occur, the plants develop into bushes 2.5 to 4 feet tall and the stems are sometimes 0.5 inch in diameter. This is several times the width of the annual stems, which, however, become quite woody by midsummer.

This species is important throughout the season. Because of its deeply rooting habit, competition with the grasses for water and nutrients is greatly reduced. The extensive woody root system extends to a depth of 6.5 to 16.5 feet. But few laterals arise until the roots reach a depth of 2 to 3 feet and it seems probable that very little absorption occurs in the surface 2 to 3 feet of soil. The lateral spread in the deeper soil is often 4 or more feet from the base of the crown, so that the root system, even if poorly branched, penetrates a large volume of soil. It is significant that nodules occur throughout the entire length of the root. Many of the tough, woody roots spread more or less parallel to the soil surface even in the first 6 inches. In plowing

the prairie these break with a characteristic snap, thus giving rise to the colloquial name of "prairie shoestring."

The great importance of this species is shown by the fact that it ranked as one of the leading societies in upland in 74 per cent of the prairies. It held second, third, fourth, and fifth rank in 6, 7, 4, and 2 per cent respectively. Only 7 per cent of the upland prairies had none. No other subdominant shows so consistent a distribution nor so great an abundance. It also occurs on lower slopes and well drained lowlands covered with the big bluestem type. In such areas it held first or second ranking only in 9 per cent but fourth and fifth in 34 per cent. It was represented in slightly over half of the lowland prairies. It is, however, much more abundant on uplands. Here it attains its greatest numbers in sandy or gravelly soil on the steeper hills characteristic of rough topography. Here also it has much to do with gradually enriching the soil and preparing a better substratum for the grasses.

HELIANTHUS RIGIDUS

Helianthus rigidus (Cass.) Desf. ranks next to *Amorpha canescens* as the most characteristic, widely distributed, and abundant of species other than grasses. It occurred in all but 13 per cent of high prairies, holding first rank in 66 per cent of them. This sunflower was also found in about half of the lowlands where it held first rank in 19 per cent. Thus its distribution is

FIG. 58. The upland prairie sunflower, *Helianthus rigidus*, showing variation in height. The smallest plant is about 15 inches tall.

FIG. 59. Single plant of *Solidago glaberrima* from moist ground. It is 32 inches high and in early bloom (August 4). Note that the lower leaves have fallen.

often rather uniform over a large area. Typically, its habitat is the uplands, and it will grow in very poor, dry soil. It begins growth in early spring, both from seed and abundant rhizomes. The root system of the seedlings develops rapidly, penetrates deeply, and at the same time forms an effective absorbing network in the surface soil. The plant spreads by means of rhizomes, making dense groups where the sod is open. This is a feature of its keen competition. The fibrous roots compete effectively with those of the grasses and extend to a depth of 5 or more feet. It is well fitted to absorb throughout the first five feet of soil.

New shoots develop rapidly. In early spring the leaves are at first spread in a rosette on the dark colored soil surface, but soon the stem elongates and may reach a height of 6 to 12 inches by the first of May. The plant varies greatly in its mature stature according to the available water content. On the drier uplands it may be only 12 to 16 inches tall, but in areas of greater rainfall southeastward more than twice this height is attained. The size of the leaves, moreover, may more than double and the number of flower heads as well (Fig. 58). A dwarfed plant with a single head and one twice its size with 3 or 4 may frequently be found within a few feet of each other where disturbance of the prairie sod has resulted in increased water content.

The lower leaves often assume a semivertical position in the grass. Even where the upper ones are very close they are so narrow and few that they cast but little shade. On the upland, after midsummer, the lower leaves usually dry and shrivel. In low ground, where this sunflower may scarcely overtop the grasses—sometimes extending the internodes to twice their ordinary length—2 to 5 pairs of the lower leaves die. Then the remaining 4 or 5 pairs of upper ones constitute the entire scanty foliage.

Over extensive areas 40 to 50 plants may occur per square meter, 60 to 70 where they are fairly thick, and sometimes 100. Since they are never densely clustered, the shading effect is not great.

This sunflower belongs to the late estival and autumnal aspects. It begins to bloom usually in the first week of July, reaches its maximum in August, and continues well into September. In dry prairies perhaps more than half of the dwarfed plants do not blossom but in lowlands flowering is more profuse. But this species of small stature can not compete well in the best big bluestem prairies and is replaced by the taller *H. grosseserratus*, *H. tuberosus*, and other coarse forbs.

ASTER MULTIFLORUS

Aster multiflorus Ait. (*A. ericoides* L.) occurs throughout much of the grassland, but reaches its greatest abundance in tall-grass prairie. Here it is especially conspicuous from the time its many white or purplish flowers begin to appear in late August or early September until the seed is ripe in

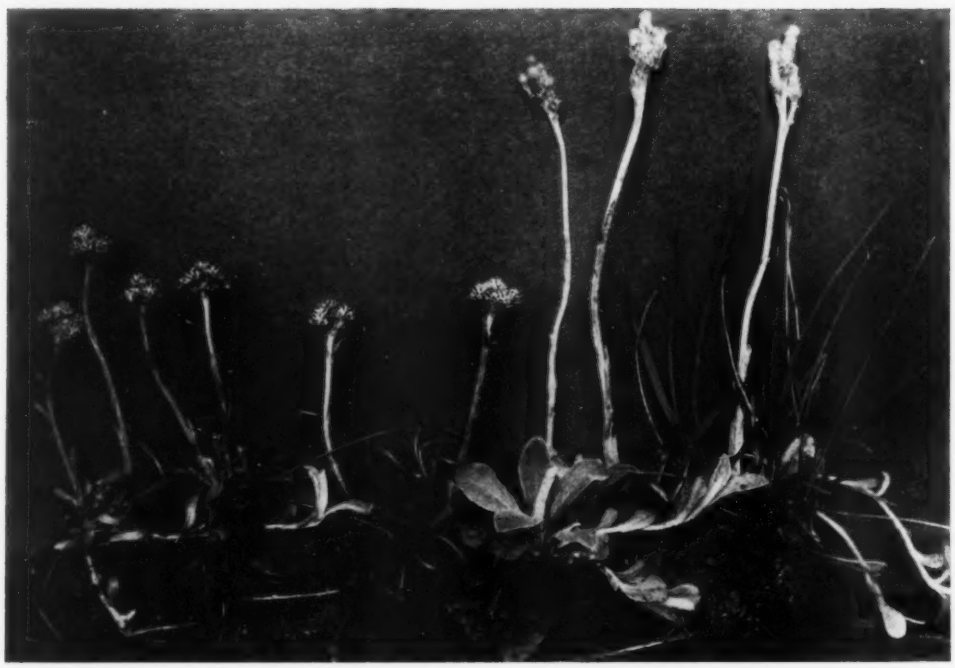

FIG. 60. *Aster multiflorus* during a dry fall when the number of flowers was reduced.

FIG. 61. Staminate (left) and pistillate flower heads of *Antennaria campestris* on May 1. Flower stalks of the latter, which are elongating after fertilization, are about 5 inches high (cf. Fig. 8).

late autumn. It is of wide-spread distribution in both dry and moist soil. In fact the more rigid, stiff-stemmed variety of lowlands is usually the form *A. multiflorus,* while the smaller, less erect one is *A. batesii* Rydb. or a closely related variety. The latter is the usual form found in drier places. This plant ranked as a leading society in uplands in 44 per cent of the prairies and as one of second or third rank in 36 per cent. In lowlands it was first in 25 per cent and held second or third rank in the same number. It was absent in one-fourth of the lowland areas but in only 15 per cent of the high prairies.

This perennial makes a vigorous new growth by the middle of April; the stems stand well above the level of the grasses in early May, and attain a height of 12 to 18 inches in June. Sometimes, especially in lowlands or denuded soil, this species develops clumps 12 to 18 inches or more in diameter and 1 to 2 feet tall. Such plants may consist of a dozen or more much branched stems, many of which lean outward in such a manner as to give the clump a bush-like form (Fig. 60). But more usually it occurs as isolated individuals 12 to 20 inches tall or in groups of only a few stems.

The clumps and individuals are connected by tough, woody rhizomes 1 to over 8 inches long. The root system is fibrous and although it penetrates deeply (7 to 8 feet) numerous finer and shorter roots absorb mostly or entirely in the surface foot of soil. The bulk of the water supply and nutrients, however, is obtained from the deeper soil, and the root system is much deeper than that of most upland grasses.

The leaves of early spring are 2 to nearly 3 inches long and 0.2 to almost 0.5 inch wide but markedly larger than the scale-like leaves of the upper portion of fully grown plants. The latter are usually only about 0.5 inch in length and 1 to 2 mm. wide, and are rather closely aggregated. Consequently, although this aster usually outranks the grass in height, yet because of its scattered growth and the small expanse of the leaves the shading effect is not pronounced. The lower leaves, moreover, are often dry and withered during summer drought to a height equaling one-third or even one-half that of the stem.

The name, many flowered aster, is appropriate, for ordinarily the heads are so densely clustered that they almost obscure the rest of the plant.

ANTENNARIA CAMPESTRIS

Antennaria campestris Rydb., the prairie cat's foot, is one of the most abundant forbs of the prairie. It was found on the upland in 78 per cent of the areas, ranking first and second in 39 and 20 per cent respectively. In low prairie it held first or second rank in only 14 per cent, and a lower rank somewhat more often. It was found, however, in only 44 per cent of these grasslands.

This species is a low mat former. It begins growth very early and thus avoids excessive competition with the grasses, most of which are slower in breaking dormancy (Fig. 8). In fact some of the leaves remain alive all winter. By the middle of March growth is resumed. Soon the dull green, brown-edged leaves of winter are easily distinguishable from the brighter green, new ones. The early activities are directed toward the production of flower stalks. Although some new leaves and stolons are also produced, yet vegetative activity reaches its maximum after the period of anthesis (Fig. 61). The species is dioecious; usually the mats or small dense communities are composed of either staminate or pistillate plants, unless they have fused. This results from propagation by stolons and rhizomes.

The heads are born on erect, almost leafless scapes usually about 2 to 4 inches long, except in dense vegetation of lowlands where they may reach 6 inches. Sometimes there are 50 to 75 flower stalks in a single square foot. After fertilization the pistillate scapes elongate to approximately twice their former length thus placing the bristly fruits in a favorable position above the grasses for wind distribution. Blossoming begins about the middle of April and continues 3 to 4 weeks, the fruits beginning to blow about by May 10. Soon they are all disseminated and the flower stalks wither and disappear. In the meantime the plants have spread by stolons and a new lot of leaves have developed.

Antennaria scarcely competes with the grasses for light but occurs almost exclusively in the bare places between the bunches and tufts of sod. The small clumps or rosettes consist of 8 to 12 leaves each. The leaves are normally about 1.5 inches long and 0.5 inch or more in width. While all do not lie flat on the ground, they seldom rise more than 1 to 3 inches above it. The plants are sometimes densely aggregated; compact mats may occupy many square meters so thickly that they actually cover 50 to even 80 per cent of the soil. More usually the mats are small and much more open. They may be only a few square inches in extent or form long, irregular patches between the grasses.

The plant is tolerant of shade, continuing vegetative activities throughout the summer even in areas of big bluestem sod. It is affected by drought more readily than most species of the prairie. During dry weather the leaves curl upward and inward so that the edges may come in contact. The lower sides of the leaves, especially, are clothed with densely matted simple hairs, which give them a woolly appearance and a grayish color. After summer drought, growth is renewed upon the advent of autumnal rains.

Antennaria plantaginifolia Hook., the plantain-leaf everlasting, a species similar in habit but with much larger and broader leaves, is occasionally found, especially in the wetter portions of the region. It flowers somewhat later in this area than the preceding species; the flower stalks are usually much more robust; and in fruit they often attain heights of 15 to 20 inches.

ERIGERON RAMOSUS

Erigeron ramosus (Walt.) B. S. P., commonly known as daisy fleabane, is a species of very wide and remarkably uniform distribution, being most frequently found on well drained soil. It is an annual or short-lived biennial, the rosettes of the first summer producing flower stalks the following growing season. It ranked as a society of the first class in 47 per cent of the upland prairies and was absent in only 15 per cent of them.

It was also present in all but one-fourth of the lowlands where it held first or second ranking in 30 per cent. Hence it forms extensive societies in the early summer aspect, its abundance varying greatly from year to year (Fig. 56).

The winter rosettes renew growth in March and by the middle of April the stems are 2 to 6 inches high. The height of mature plants varies greatly; sometimes they begin to blossom when only 8 inches tall, but usually they are 1.5 to 2 feet. Since blooming begins near the end of May, the plants show conspicuously above the grasses. The number of flower heads varies widely; often there are 25 to over 100 on the branched top of a single plant. Blooming ordinarily continues until the middle of July, but on low ground somewhat longer. In areas of moderate density 25 to 50 plants occur per square meter, but where thickest 100 to 125 are found.

The plants are mostly single stemmed but some have 2 to 5 stalks. Their intolerance to shade is shown by the early death of the lower leaves. By midsummer the whole plant may wither and die but sometimes they remain alive until fall. The stems are only moderately well clothed with the narrow leaves and branching occurs well above the general grass-level. Hence even where the plants are thick they have little effect in shading the grasses.

Erigeron annuus (L.) Pers., although often abundant locally, is much less widely distributed and of far less importance. It occurs mostly in the moister soils and is of greatest abundance in the areas of higher rainfall.

SOLIDAGO GLABERRIMA

Solidago glaberrima Martens, the Missouri goldenrod, is the most widely distributed and most important of the numerous goldenrods of the prairie. It is a coarse perennial that spreads widely by means of stout rhizomes, mature plants among the grasses reaching a height of 1 to 3 feet (Fig. 59). The stems ordinarily are not densely clustered, but form an open growth with the individuals from the rhizomes 2 to 6 or more inches apart. The rosette-like clusters of leaves which grow after early autumn mowing remain alive over winter, at least during mild ones, and renew growth fairly early in spring. By the first week in May they are often 5 to 8 inches high and stand out conspicuously above the grass level (Fig. 41). Indeed, where they occur abundantly the vigor and density of the grasses are considerably reduced; 50 to

75 stems per square meter often occur, and where thickest 100 to 125. The height attained varies greatly, from 8 inches in poor soil in dry uplands to 12 to 30 inches over the high prairies generally. In large plants the stems are 5 to 8 mm. in basal diameter and quite woody. The size of leaves is variable ranging from 2 to 4 inches in length and from 0.5 to over 1 inch in width. The stems may be leafy to the base or because of drought or deep shade defoliated by midsummer to a height of 6 to 24 inches. Blossoming begins late in July and helps to usher in the autumnal aspect. Then the prairies are aglow with the yellows of various goldenrods and sunflowers, and, a little later, the purple of the blazing stars.

This goldenrod occurred in all but 24 per cent of the upland prairies. It held first, second, and third rank in 32, 12, and 20 per cent, respectively. In the big bluestem prairies it was much less abundant, being absent in 56 per cent of them and holding first or second rank only in 15 per cent.

PSORALEA ARGOPHYLLA

Psoralea argophylla Pursh is a legume that forms estival societies throughout much of the prairie. It has a strong, moderately deep taproot which is poorly branched. This may account in part for the fact that it grows best on lower slopes where water content is greater than on the higher lands.

Psoralea forms extensive societies especially on the lower hillsides and steep slopes along ravines and is usually distributed over well drained, moist, level lands (Fig. 37). It is not ordinarily found in the little bluestem type proper but where the water content is such that this integrades into a mixture with the big bluestem sod. In the drier, level lands of South Dakota the plants were found as somewhat widely scattered individuals rather than in the usual social groupings.

This silvery Psoralea was present in 74 per cent of the upland prairies and held first rank in 37 per cent of them. In low prairies it was less widely distributed, occurring in 43 per cent. It ranked first in 8 per cent but had a higher percentage in both fourth and fifth places. This is in agreement with its more frequent occurrence and greater abundance in the drier grasslands of the general area.

The plants are of a bright leaden or silvery color and 12 to 28 inches in height when mature (Fig. 74). They are nearly always single stemmed and have practically no leaves to a height of 6 to 12 inches. But they develop a branched, open crown 5 to 10 inches wide. This forms a well-lighted upper layer for food manufacture. Even where 30 to 60 individuals occur per square meter, as is often the case in well developed societies, they seem to be only slightly detrimental to the grasses. In fact the grass appears normal in density after these legumes have been removed.

The naked shoots appear early in April and the leaves unfold several inches above the soil level. Blossoming begins about the first of June, but

this society is conspicuous because of its silvery foliage rather than its small, blue flowers. Late in summer an abscission layer causes the stems to break near the soil surface and the tops tumble over the grasses as they are driven by the wind. The seeds are thus widely distributed.

OTHER SPECIES

Achillea occidentalis Raf. is a stout-stemmed composite that, owing to its rhizome habit, frequently grows in rather dense clusters. This is especially true where there has been some disturbance such as grazing. This species readily becomes a noxious weed. Moreover, the broad, usually white-flowered, flat-topped corymbs appear conspicuously even if the plants are not abundant. This perennial renews growth by the middle of April and during anthesis in June is about 2 feet tall. It was found in half of the uplands, usually with a low ranking, and in only 40 per cent of the low prairies where it was even less important.

Anemone cylindrica A. Gray is a characteristic though usually not abundant plant of the prairies. The long petioled, 3 to 5 parted, basal leaves form a small cluster while the cauline (involucral) ones of similar habit are held above the general grass-level on long slender stems (Fig. 62). The greenish white flowers of June and July are few in number and of small size. They are less conspicuous than the elongated fruiting heads that are clothed with cotton-like achenes. This long-fruited windflower occurred in 40 per cent of upland prairies. It is typically found on lower slopes, along ravines, and on low ground westward but gradually ascends as precipitation becomes greater and occurs eastward also on hilltops. Only in 3 per cent of the prairies did it occur as a society of first or second rank but most often in fifth place. On lowlands, however, it held first rank in about half of the prairies in which it was found.

The prairie mugwort, *Artemisia gnaphalodes* Nutt., is a conspicuous plant of the grasslands both because of its social habit due to rhizome propagation and its whitish appearance against the background of green. The latter is due to a dense coat of hairs, which can be removed by rubbing, thus exposing the green leaves. Renewing growth with the grasses about April 15, it always overtops them and is 12 to 15 inches high by the middle of June (Fig. 40). Until midsummer the stems are leafy to the base. A single square meter in a moderately dense area had 150 plants (stems) and they are sometimes twice as numerous. During their growth throughout the summer they use much water and considerably shade the other vegetation. When they are removed it is plainly seen that the remaining plants are only about three-fourths the normal density.

This sage is rather local in its occurrence, but where it is found the plants are often aggregated. In the drier types of high prairies it occurs mostly on lower slopes and bordering draws. Frequently it forms dense, gray

patches in broad ravines and even in the margins of slough-grass areas. Eastward it occurs frequently and sometimes abundantly on moist slopes or level uplands. Although often ranking as a first class society in both types of grassland, it is represented much more frequently by societies of the third and fourth class. It was found in all but 30 per cent of the high prairies

FIG. 62. A fine specimen of *Anemone cylindrica* about 2 feet tall and in fruit, July 10.

FIG. 63. Mature plants of *Artemisia gnaphalodes* 2.5 feet tall, on Sept. 1. The lower leaves have died as a result of shade and drought.

and in 56 per cent of the low ones. Mature plants are very leafy and the tops much branched (Fig. 63).

Asclepias tuberosa L., the pleurisy-root, although not abundant, is one of the most conspicuous of prairie species. The stems from the large, woody crown are 2 to 3 feet tall, coarse, and very leafy from near the base. They occur in groups of 15 to 50. Thus an individual plant often has a spread of tops of 2 to 4 feet. The grasses about such a clump are always held in check and beneath it there are none. When the very large, orange-yellow to brick-red, many flowered umbels develop, the sight is especially pleasing.

Adding to its beauty are numerous varicolored visiting butterflies hovering over the flowers. This phenomenon is so conspicuous that it easily accounts for another common name, butterfly-weed.

This milkweed is typically found near the foot of steep, well drained slopes but also occurs on the uplands and hilltops eastward. It is not gregarious in its habits and where thickest there is rarely more than one per square meter. Usually only isolated individuals are found. This accounts for its frequent rating in fourth and fifth places both in high prairie (11 and 23 per cent) and in lowlands (11 and 19 per cent). It was listed in 35 per cent of the uplands and in 30 per cent of low areas. The plant remains green until frost.

Aster azureus Lindl. and *A. sagittifolius* Willd. are both common in the prairies but are far more abundant in those with higher rainfall. The sky-blue aster is the more important. It reaches a height of 1 to 4 feet, the stems branching above and giving rise in late summer and autumn to a wealth of bright blue flowers. This perennial arises from a thick rootstock and the stems which are often 4 to 10 in number are usually more or less grouped. The abundant, broad leaves are 2 to 6 inches long and cast considerable shade. It is very tolerant of shade.

The arrow-leaved aster is less common but frequents prairies near woodlands. It is also perennial and possesses strong rhizomes. It makes an early rapid growth and reaches a height varying from 2 to 5 feet. This species usually stands well above the grass level so that the great racemes of light blue or purplish flowers show conspicuously in the autumnal aspect. The large basal leaves are mostly sagittate and quite tolerant of shade. Although of minor importance over the prairies as a whole, these asters ranked as societies of the first class in 5 per cent of the uplands and held a lower ranking in 8 per cent.

Aster laevis L. is a tall perennial found mostly on the uplands of the more moist eastern and southeastern parts of the area. It spreads by means of thick rootstocks, the stout stems, which are 1 to 4 feet tall, being either simple or little branched. The leaves are variable in appearance and habit. The young leaves are somewhat glaucous but later they become dark green. While the upper ones are sessile, more or less cordate and auriculate clasping and those of the branches small and often bract-like, the lower ones are larger (often 4 to 8 inches long) and have winged petioles. During September and October this smooth aster puts forth a wealth of blue or violet flowers. By this time many of the basal leaves have fallen as a result of the dense shade of the grasses notwithstanding the fact that this species is very tolerant of shade. This aster occurred in about one-fourth of the high prairies, but in only 9 per cent of the lowlands. It ranked as a society of the first and second class in 13 per cent of the former. Sometimes the stems

occur singly but they are usually grouped; 5 to 10 or more stems arising from a single root-crown.

Astragalus crassicarpus Nutt. (*Geoprumnon crassicarpum* (Nutt.) Rydb.) is a characteristic species of well drained, upland soil where it sometimes holds the place of a society of the first rank. Its wide distribution is shown by the fact that it occurred in 47 per cent of the prairies with a ranking as regards first to fifth place of 10, 13, 13, 12, and 9 per cent. In well developed societies the plants vary from 3 to 10 per square meter, including well established seedlings. It was found in only 9 per cent of the low prairies, and never ranked above fifth place. This Astragalus is a large, coarse, decumbent plant, especially conspicuous in spring and early summer before the grass has grown above it. Its abundant, large, violet-purple flowers add to its conspicuousness, as do also the numerous fruits or "ground plums" (Figs. 6 and 19).

A single plant has 7 to 30 stems and especially large specimens as many as 75. These coarse, somewhat fleshy branches are mostly greenish, but frequently reddish in color. They spread widely, more or less covering a circular area 2 to 3 feet in diameter. The compound leaves are widely spaced and the small leaflets do not cast much shade. The branches are often so densely grouped, however, that the total shading effect is marked, and circular bare areas 6 inches in diameter are often found when the plant is removed. More often, however, the grasses are little retarded in their growth and by early July this legume is more or less obscured by them. By fall, nearly all the plants' parts above ground have disappeared.

The ground plum renews growth in March. Drawing upon a large food supply stored in the crown and coarse taproot, it develops rapidly and is in full bloom a month later. The flowers, which are an inch or less in length, usually occur in clusters of 8 to 20. Often 100 or more such clusters are found on a single plant. They occur from near the soil surface to a height rarely exceeding 8 inches, and lend a pleasing variation to the greenish background of the young grasses. By the middle of May fruits begin to appear. Frequently 50 to 150 are borne by one individual. When fully grown, in June, they are nearly an inch in diameter, somewhat longer than wide, and beautifully colored with a blotch of red on the upper side. The fruits later dry in the sun and may be found the following winter and spring clustered about the base of the dead stems still retaining the few, small seeds.

The size of the fruit is a good index of the water relation of the habitat as is also the stature of the plant. In areas of lighter rainfall westward and northward and especially during years of drought the size both of fruit and plant may attain only two-thirds or even one-half that of those in prairies with a better water supply. As regards height, this species rarely exceeds 12 inches in the little bluestem or needle-grass sod, even after it becomes more erect as the grasses grow above it. But on lower ground where it is inter-

mixed with taller grasses, a height of 15 to 18 inches is attained. While there is some competition above ground for light, the plant demands little after its period of anthesis. Below ground there is little competition since absorption occurs mostly at considerable depths (2 to 8 feet) and largely below the absorbing zone of the upland grasses.

Baptisia leucantha T. & G. is a unique species of the prairie. The fully grown plant with single stem and widely branched crown resembles a miniature tree standing 2 to 4 feet above the general level of the grasses. Its large, cream-colored flowers occur in conspicuous racemes and the inflated, small seeded pods are an outstanding feature of the lower slopes where the plant is mostly found. But if the rainfall is sufficient it grows upon the hills as well. The plants are nearly always widely scattered and only rarely are they very abundant. They have no harmful shading effect upon the grasses (Fig. 43).

Baptisia leucophaea Nutt. is a large, coarse, widely spreading perennial that occurs in about half of the upland prairies but rarely in great abundance. Its highest rating was as a society of the fourth class (21 per cent) and it attained first or second rank in only four per cent. It was found sparingly on 20 per cent of the lowlands. In the north and west this species occurs usually on lower slopes where drainage is good, but in the better watered prairies southward and eastward it is also commonly found on hilltops as well.

The plant consists of 2 to 12 thick stems which branch 3 or more times at a height of 6 to 8 inches. It spreads widely so that the tops of well developed specimens are 2 to 3 feet in maximum width. The height is usually 1 to 1.5 feet and since the plant makes its growth early in the season the leafy top is well above the grass-level, which makes it very conspicuous. When blossoming begins, early in May, the big racemes of large cream-colored flowers extend conspicuously beyond the foliage (Fig. 64). Flowering begins a week or two after the leaves have unfolded, a development which takes place only after the thick, naked shoots have rapidly grown to a height of 4 to 8 inches. The large, inflated pods, 2 to over 3 cm. long, with their small seeds are fully formed late in June; 12 to 24 fruits may occur on a single raceme.

In small individuals the tops are open and the grasses are shaded only a little, but where large, bushy plants occur in groups, as sometimes happens, the shade is fairly dense; the removal of the legume reveals small, bare areas near its base. The name "false indigo" is derived from the fact that when a part of the plant is crushed, the sap, upon exposure to the air, takes on a dark purple color. Although some of the plants remain green or partly so all summer, yet more often after midsummer the leaves dry, the stems break near the ground line, and the tops are blown away by the wind, often at a high rate of speed. Thus possession of the area above ground, by this widely spaced species, is not permanent.

FIG. 64. False indigo, *Baptisia leucophaea*, in full bloom on June 1 at which time it quite overtops the grasses.

FIG. 65. *Ceanothus pubescens* in June. The plant is only about 2 feet tall since it was cut the previous fall in mowing the hay.

The taproot system is very characteristic, the older portions being greenish yellow, the younger ones orange in color. From the base of the thick crown the roots spread obliquely and run downward in such a manner that the maximum lateral spread is about 1.5 to 2 feet from the base of the crown. Little absorption occurs in the first 2 or 3 feet of soil. The roots penetrate 8 or more feet in depth and depend largely upon the subsoil for their water and nutrients.

Ceanothus pubescens (T. & G.) Rydb. is a low shrub, with many stems 1.5 to 3 feet in height. It is one of the more important species of the prairie and has a wide distribution (Fig. 65). It is characteristic of uplands, always reaching its greatest abundance on dry hillsides and ridges, and is never found on lowlands and rarely on lower slopes. It was found in 40 per cent of the upland prairies where it held each ranking from first to fifth in 8 per cent. Often as many as 50 to 200 stems arise from the enlarged woody crown. These spread widely so that although the basal area may occupy only a square foot or less, yet the top may have a spread of 5 or more feet. Usually, however, the clumps occupy a smaller space. While in some places only isolated plants are found, yet where best developed, in local areas, they may constitute one-fourth to one-third or even more of the vegetation. Where the stems are few and the plants scattered, the grasses grow up between them, but where larger bushes are thick—often 3 or 4 clumps with 20 to 30 stems each per square meter—the shade is dense. Moreover, the lower leaves to a height of a foot or more fall by midsummer and form a mulch upon the ground. Where the bush is removed an area 2.5 to over 3 feet in diameter is found to be free from grasses, or at least only partially occupied by the shade enduring bluegrass. Although held in check by annual mowing, a considerable growth of Ceanothus materially reduces the yield of hay.

The plants are long-lived. One specimen, 13 years old, had a woody taproot 1.5 inches in diameter and over 15 feet deep. The root system spreads very widely and is well branched throughout. Many roots also occur in the surface soil. Thus this species competes with the grasses for water as well as for light. It resumes growth about the same time as the bluestem grasses, i.e., the middle of April. Blossoming begins early in May and continues about 5 weeks, although some blossoms may be found throughout the summer. The plants remain green until frost.

Coreopsis palmata Nutt. is a perennial composite that propagates extensively by rhizomes. While it is not uncommon to find only a few plants in an area, still they are usually more or less densely aggregated into conspicuous societies. The stems of this stiff tickseed are fairly rigid, 1 to 3 feet tall, and either simple or little branched. They are very leafy. The characteristically deeply 3-lobed leaves (sometimes with 5 to 7 lobes) are opposite, sessile, and 2 to 3 inches long. Where the plants are few they have little effect upon the

grasses; but where there are 6 to 10 or more stems per square decimeter the stand of grasses is reduced one-third to one-half or more. Where the societies are densest, very little other vegetation occurs in areas 15 to 25 feet square. Coreopsis is very tolerant of shade and becomes defoliated only a little near the base. The yellow flower heads, usually 3 or more per plant, appear during the estival aspect and persist for only a few weeks. It is distinctly an upland species and occurred in 27 per cent of the prairies, ranking as a society of the first class in 15.

Delphinium virescens Nutt. occurred in 36 per cent of upland and 32 per cent of lowland prairies. It never ranked higher than a third class society and held third place only a few times.[8] On both uplands and lowlands it was found most often as a species of very limited occurrence. This tall prairie larkspur has a stout stem which arises from a thick, woody root. The deeply cleft leaves are not numerous, and the usually isolated or widely spaced plants are conspicuous largely because they stand so prominently, usually 1 to 2 feet, above the general level of the grasses. The large, white flowers, sometimes tinged with bluish spots, appear mostly in May and June. These with the conspicuous fruits readily attract attention (Fig. 107).

Echinacea pallida (Nutt.) Britton is a coarse composite of the early summer aspect, which thrives best on dry hilltops and other well drained uplands (Fig. 66). The plant usually consists of 2 to 5 mostly simple stems, each with a single, terminal flower head, which spring from one root. The stems are 18 to 24 inches high and thus stand well above the grasses. Although the plants have 3 to 10 coarse basal leaves, these are more or less erect and usually the groups are so open that the shading effect is almost negligible, especially since the leaves are overtopped by the grasses. The coarse, scabrous, cauline leaves also assume a somewhat vertical position. In better watered areas eastward, as many as 10 stalks occur per plant. These large plants are 30 to 40 inches tall, the diameter of the stem is often twice the usual thickness, and the flower heads are proportionately larger. They form a striking contrast to the dwarfed plants with only 1 or 2 stems found in the driest prairies. Although widely spaced plants are common, yet where thickest 6 to 8 may occur per square meter.

Growth begins early in April, proceeds rapidly, and by the middle of June the large purple flowers (nigger heads) are abundant. They are usually 7 to 8 cm. in diameter, but in rich, well watered soil in Iowa and Missouri, the ray flowers alone may be 7 cm. long. Flowering lasts about a month but the black central cones are conspicuous until late fall.

Echinacea propagates only by seeds. The seedlings grow slowly; often three years are required to accumulate enough food for the little rosette to put forth a flower stalk. It is very tolerant of shade. The rather large, fleshy, and

[8] A few species such as *Delphinium virescens*, *Asclepias tuberosa*, *Gentiana puberula*, etc., form clans rather than societies but for convenience they are ranked with the societies (cf. Clements, 1920).

FIG. 66. *Echinacea pallida* (nigger heads) about June 20. Plants of *Helianthus rigidus* in left foreground.

FIG. 67. Flowering spurge, *Euphorbia corollata*, (left) on June 24. It is 3.5 feet tall and in early bloom.

FIG. 68. Two plants of *Hieracium longipilum* about 3 feet tall on July 30.

somewhat woody taproots are poorly supplied with branches, but they penetrate deeply, usually 5.5 to 8 feet.

This species was found in all but 34 per cent of upland prairies and the ranking of a society of the first importance was held in 20 per cent of them. It was found in less than one-fourth of the big bluestem prairies where it usually ranked fourth or fifth and never above a society of the third class.

The flowering spurge, *Euphorbia corollata* L., is a species of much prominence and wide distribution in the southeastern half of the area. In the drier part it occurs rather infrequently even on lowlands. It was absent on 65 per cent of lowlands, and ranked first in only 8 per cent, but fifth in 16. On uplands where it was present in 40 per cent of the areas, it held first place in 20 per cent of them.

This tall perennial occurs mostly as single stems, 3 to 5 feet high, but is often grouped in clusters of 2 or 3 and sometimes as many as 30. It propagates by long, stout rootstocks. The lower leaves are scale-like to a height of about 6 inches. The leaves in the grass fall from the base of the stem and those remaining above are small and not widely spreading. By the middle of July many of the wand-like stems terminate in a whorl of branches bearing the numerous white flowers (Fig. 67). The umbels are 3 to 7 forked, and the forks again divide into 2 or 3 branches. It is at the time of blossoming that this species is such a conspicuous feature of the landscape. Often 5 to 20 individuals are found in a single square meter.

The hawkweed, *Hieracium longipilum* Torr., stands in midsummer as a lone sentinel found only here and there in almost any prairie, particularly in dry ones. It occurred in but 15 per cent of lowlands. In uplands it did not attain higher than third rank and this in only 6 per cent of the areas. In 14 per cent it was rated fourth, and in 17, fifth. But notwithstanding its small numbers it is a very characteristic species. The central stem of the rosette of hairy leaves stretches up to a height of about 3.5 feet during the latter half of July (Fig. 68). The wand-like upper half is practically free from leaves. The small, yellow flowers are less conspicuous than the hoary pappus of the ripe achenes. Blossoming may continue into September.

The false prairie boneset, *Kuhnia glutinosa* Ell. (*K. suaveolens* Fresen.), is an important composite, especially of upland prairies (Figs. 6 and 12). Here it was found in all but 22 per cent. It ranked first in 16 per cent of these prairies and in the other classes 3, 18, 28, and 13 per cent, respectively. This shows its wide distribution and high constancy. On low prairies it was present in only 30 per cent, and its highest rating was as a society of the second class (11 per cent). It does not grow in poorly drained soil.

Kuhnia produces an abundance of seed which are well adapted for carriage by wind. The seedlings grow rapidly and vigorously developing many branches and numerous broad leaves. Unless competition is too severe they may reach a height of 16 inches and a few may blossom the first summer.

During this period the taproots have branched widely and penetrated 2 to 2.5 feet into the soil. By the second autumn a single plant may have 6 to 10 stems and fruit abundantly.

Growth begins early in May, the numerous shoots arising from the multicipital stem on the strong taproot. The latter is larger and deeper than that of most plants of the prairie. It is usually 0.7 to 1.5 inches in diameter and 16 or more feet deep. It competes but little with upland grasses for water and nutrients because its well branched laterals absorb throughout a large volume of soil far below.

Mature plants, some perhaps 25 to 30 years old, attain large size—often a basal diameter of 6 to 8 inches, a height of 3 to 3.5 feet, and a spread of tops of 2 to 3 feet. Such bunches have more than 100 stems. They drive out the prairie grasses, bluegrass alone being able to tolerate the low light intensity. In large clumps the upper leaves alone make food at the normal rate, the middle ones only about one-half as fast, while the still lower, half-yellowed leaves do not receive enough light to carry on photosynthesis. This is shown beautifully by bleaching the leaves in alcohol while they are still attached to the stem and applying Sach's iodine test.

This species is quite as characteristic in the vegetative stage as in blossom. It belongs to the autumnal aspect and is most conspicuous when in fruit. The white-hairy achenes occur in enormous numbers and are widely distributed by the wind.

Lespedeza capitata Michx. is a tall, erect or ascending legume with a stiff, mainly simple and wand-like stem. The stems occur singly or usually only a few from a single root. The height of the plant, 2 to 5.5 feet, and the abundance of the silvery, silky pubescent, trifoliolate leaves make it conspicuous even where it is not abundant. In the drier parts of the area it is found mainly on lower slopes and well watered low ground, but elsewhere it occurs widely. The roots are much branched just below the soil surface. They penetrate 2 to 3 feet on all sides of the plant. Then the main branches may turn downward, and like others beneath the stem penetrate 5 to 8 feet deep. Thus it is well fitted for both dry and moist soils.

It was found in 55 per cent of the upland prairies and also in approximately the same number of lowlands. Its ranking as a society of the higher classes, however, was a little greater on the uplands. In a few cases as many as 46 plants occurred per square meter; they were usually much fewer and bulked largest as societies of the third and fourth class. Since the total spread of the foliage on a stem is only a few inches and the base of the stem is defoliated, this plant has little harmful effect upon the grasses. The dense, globose flower heads, which are sessile in the upper axils, appear in August or September. The yellowish white corollas are not very conspicuous, in fact no more so than the dark brown ripened "heads" of this round-headed bush clover.

Several species of Liatris occupy a prominent place in the vegetation of the prairie and add grace and beauty to the autumnal aspect. Among these *L. punctata* Hook. is one of the most important. This is a coarse, perennial composite well adapted by its long life, extensive root system and limited foliage of harsh narrow leaves to grow in dry soil (Fig. 69).

Seedlings grow very slowly above ground but with marked rapidity below. By midsummer they may be only 5 inches tall and have but two, long, narrow,

FIG. 69. A blazing star, *Liatris punctata*, on Sept. 1.
FIG. 70. *Liatris scariosa* 3.5 feet tall and in early bloom on Sept. 1.
FIG. 70a. *Liatris squarrosa* beginning to bloom on August 1.

erect leaves, but the taproot is 2.5 to 3 feet deep. It is extremely tolerant of shade, growing under light intensities of only 5 to 10 per cent. Food is stored in the fleshy taproot only a few weeks after growth begins. In fact, the plant becomes so firmly established, that few die after the first winter, unless disturbed by rodents. It may require three or more years for the production of flower stalks, but this is a small part of the life span of this species which may well live 50 years.

The plant has a thick taproot. The stems are often few (3 to 10) and the clump correspondingly small but on large plants 50 to 70 have been counted. Here the base occupied an area 5 to 8 inches in diameter and the widely leaning stems caused the top to spread 1.5 to 2 feet. All but the most tolerant grasses disappear under such clumps. Height varies greatly with water content and surrounding vegetation. On dry years, westward it may scarcely exceed 16 inches; 2 to 2.5 feet is usual, but well developed plants 5 feet tall have been found in Iowa.

The taproot is remarkably extensive; its branches spread laterally 3 to 4 feet and penetrate very deeply. The generalized root system more or less

thoroughly occupies the first 8 feet of soil, absorbing little in the first foot, and sometimes reaching a depth of 16 feet.

The preference of this species for drier habitats is shown in its general distribution, being more abundant in the drier soils westward. In fact, it is entirely absent in many of the prairies northeastward. Locally, gravelly ridges, dry slopes, and well drained uplands are its abode.

This dotted button-snakeroot was found in about 58 per cent of the upland prairies where it ranked first in 10 per cent. It was rarely found on low ground.

Liatris scariosa (L.) Willd. (*L. aspera* (Michx.) Greene) was found in nearly two-thirds of the uplands and in 16 per cent of low prairies. In the latter it was seldom abundant; in high prairie it held first rank in 14 per cent, and second, third, and fourth in 8, 17, and 16 per cent, respectively. The stems are frequently solitary, often in two's or three's, but sometimes 8 to 12 arise from a single large corm (Fig. 70). The corm of old plants is 3 to 4 inches in diameter and very irregular in outline. It gives rise to 25 to 100 nearly vertical basal leaves and to numerous, tough, fibrous roots. Even in year-old seedlings the roots extend to a depth of nearly 4 feet. This has developed while the seedlings are as yet only 4 to 6 inches tall and well illustrates the habit of prairie species of making early, ample provision for a sufficient water supply.

This species ranges in height from 1 to 5.5 feet. The linear leaves, especially the basal ones, are 7 to 12 inches long and fairly broad, although they are reduced to mere bracts near the inflorescence. The flower heads, which are mostly 2 cm. or less in diameter, usually occur abundantly, often 50 to 100 or more on a single stem. The wealth of rose-purple flowers as well as the colored tips of the large bracts form a pleasing and impressive sight. Although frequently occurring as isolated individuals, yet sometimes as many as 15 plants are to be found in a single square meter. Notwithstanding the fact that it is an autumnal bloomer, yet like the other blazing stars it makes a vigorous growth in May and maintains its place among the grasses throughout the entire year.

Liatris squarrosa (L.) Willd. (*L. bebbiana* Rydb.) is confined largely to the uplands of the eastern part of the area. Here it was found in 17 per cent of the high prairies and ranked first or second only in 3 per cent. It varies considerably in size and greatly in abundance, sometimes being the most conspicuous species on a dry ridge or hillside. The plants vary in height from 6 to 24 inches. The stems, which are clothed to the base with rigid, linear, elongated leaves, occur in small to large groups, often 10 to 30 per clump (Fig. 70a). Sometimes 3 to 5 of these clumps were found to the square meter. Large bunches of 100 to 150 stems were also found, where from a basal diameter of 6 or more inches the tops spread 1 to 3 feet. They cast so dense a shade that when they were removed, except for a light sprinkling of bluegrass, there was a bare area 6 to 12 inches in diameter. The rose-

purple flower heads, which are narrow and not large, appear in August, and where the plants are at all abundant, add much to the beauty of the autumnal aspect.

The yellow flax, *Linum sulcatum* Riddell, is a species of minor importance but one that is widely distributed on uplands. Here it occurred in more than half of the prairies, but ranked almost entirely in third and fourth places. The plants are often single stemmed and almost unbranched; sometimes in low areas they have 4 or 5 stems and each stalk 5 to 7 branches. In height they overtop the grasses. Where thickest, 50 to 125 plants have been found per square meter and the whole hilltop was yellow with blossoms. Such abundance is unusual. But even here the short, narrow, linear, erect leaves are so closely appressed to the stem that the species has little effect upon the surrounding vegetation. This flax blossoms from late June into September.

The genus Meibomia is represented widely in the prairies by only two species. They are so similar in their early vegetative growth that societies were not readily distinguishable with certainty, hence they were not listed separately. During flowering and fruiting it was clearly apparent, however, that *M. illinoensis* was the more abundant, especially in the western half of the area, while *M. canadensis* was a species of much importance and wide distribution in the eastern part. There is, of course, considerable overlapping in their ranges, and on some prairies both species may be found in abundance. They are rather similar ecologically in many ways, a chief taxonomic difference being certain characters of the jointed loments.

Meibomia illinoensis (A. Gray) Kuntze is a tall, coarse herb furnished with numerous, large, pinnately 3-foliolate leaves (Fig. 71). It grows slowly in spring and by June 1 is often only 6 to 8 inches high. But the leafy stalks develop rapidly thereafter, and the long, terminal racemes that appear about July 1 ultimately reach heights of 5 to 6.5 feet. Soon after the small purple or purplish flowers appear the lower loments are formed. Late in July they begin to adhere to one's clothing and later they are a veritable pest where the plants are at all abundant. By early September most of the leaves are dead and have fallen, relatively few remaining green. The plants usually form clumps ranging in size from 3 to 8 stems to much larger ones southeastward with a basal diameter of 7 to 14 inches and a spread of tops of 1 to 2 feet. They are very tolerant of shade and leafy to the base. When they are removed it may be seen that the grasses are absent in the immediate area occupied by this tick-trefoil.

In the drier part of the region Meibomia is confined to draws or low ground, but eastward it occurs also on uplands. It is scattered widely throughout the grasses, there rarely being more than 4 or 5 plants per square meter.

The Canadian or showy tick-trefoil, *Meibomia canadensis* (L.) Kuntze, has shorter petioles and nearly sessile upper leaves. The flowers are often

1.5 cm. long, purple or bluish purple, and very conspicuous. They appear somewhat later than those of the preceding species and add not only to the estival but also to the beginning of the autumnal aspect. The plants, moreover, tend to grow in larger clumps. For example 35 or more stems are frequently grouped to form clumps with a basal diameter of more than a foot. The stems, which are 4 to 7 feet tall, spread widely at the tops (Fig. 72).

Although these two species occurred in as many upland prairies as low

FIG. 71. *Meibomia illinoensis* 6 feet tall and in flower and early fruit. The tops are erect in nature.

FIG. 72. A large plant of *Meibomia canadensis* with *Liatris pycnostachya* 6 feet tall just back of it. Anita, Ia., July 22.

ones (42 per cent) yet they ranked first or second in importance in 15 per cent on upland and 25 on lower ground. They were often found in both areas as societies of the third or fourth class.

Morongia uncinata (Willd.) Britton (*Leptoglottis nuttallii* DC.), the sensitive brier, although entirely confined to the southern part of the territory studied, is a species of considerable local importance. This legume is decumbent, the width of the prostrate plant varying from 3 to 5 or more feet. It forms a dense growth on well drained slopes and uplands and very seriously handicaps the growth of the grasses. All parts of the plant are thickly armed with hooked prickles. Hence it is not eaten by stock and reduces the value of the hay. The large, pinnately compound leaves are sensitive to touch, closing when disturbed and revealing the outlines of the rather woody, coarse stems. The great abundance of pink flowered, globose heads, in June and July, as well as the rather large spiny pods help to make this species conspicuous. It oc-

curred, often as a society of the first or second rank, in only 15 per cent of the upland prairies.

Pedicularis canadensis L. is a low, perennial species of rather infrequent occurrence in prairies, but of much interest because of its indicator significance. Only rarely is it found in low prairies as scattered individuals among the big bluestem. It is typically an inhabitant of thin, sandy or gravelly soil, or one where seepage may occur. This lousewort nearly always occurs as

FIG. 73. Two prairie clovers about 2 feet tall; *Petalostemon purpureus* (left) and *P. candidus* in early bloom, July 10.

FIG. 74. A single plant of *Psoralea argophylla* 8 inches tall and in bud. Photo. June 1.

densely aggregated groups of a few feet or yards in extent but it may recur repeatedly in an area offering favorable habitats. Where best developed, almost no grass is found except *Poa pratensis*. It is also sometimes scattered in the little bluestem sod or may be found at the edge of areas of Spartina. The large, pinnately lobed leaves and yellow or reddish flowers on these usually low-growing plants are very noticeable in May and June. The characteristic patches occur as islands in a sea of grassland. It was found in less than a score of prairies, usually in the more mesic uplands eastward.

The prairie clovers, *Petalostemon candidus* (Willd.) Michx. and *P. purpureus* (Vent.) Rydb., are widely distributed and important legumes (Fig. 73). Both are often extremely abundant, especially southward. In very open stands 5 to 10 plants may occur per square meter, 50 to 60 are frequent, and in well developed societies the number is even larger. Usually there are only 1 to 3 stems per plant, but sometimes 10 to 12 may arise from

a single root. Occasionally bunches 7 inches in basal diameter with 60 stalks and 30 to 50 flower heads occur.

Beginning growth with the grasses, they soon outstrip them in height. By the middle of June they are 18 to 22 inches tall, and extend upward to 2 to 2.5 feet when blossoming begins about the first week in July. The conspicuous heads, 0.5 to more than 2.5 inches long, are terminal on the branched tops and stand far above the general level of the grasses. After the blossoms have disappeared the dark cones are conspicuous until late autumn. Only when the plants are large and closely spaced do they cast much shade. Ordinarily they are far enough apart so that the small leaflets let most of the sunshine pass. Moreover, by midsummer the stems are defoliated to a height of several inches. The leaves of *P. purpureus* are smaller than those of *P. candidus* but clothe the stem more thickly. The leaflets fold somewhat during drought.

Both species propagate by seed. The seedlings grow rapidly, reaching a height of 6 to 9 inches by midsummer. Sometimes blossoms occur the first year, and regularly the second, providing there is no unusual drought. By midsummer the taproot has extended downward 14 to 22 inches. The mature white prairie clover has a strong, deep taproot. It extends downward 3.5 to 6 feet. The root system is well branched, especially the deeper portion; but there is not much absorbing surface in the shallower soil. The taproot of the purple prairie clover gives rise to laterals that are minutely branched and compete with the grasses for water in the surface soil. Some of the laterals spread horizontally a foot or more before turning downward. Depths of 4 to 6.5 feet are attained.

Although these species often grow in mixed societies, yet the purple clover prefers higher ground. Since one can not readily distinguish between societies of the two species in their early growth, their distribution was not recorded separately. Very frequently they occur together; but northward, at least, the white flowered species is far more abundant.

On uplands these legumes were present in three-fourths of the prairies. They ranked as societies of the first, second, and third class in 22, 17, and 13 per cent of these grasslands and occurred in fourth place in one-fifth of the areas. In low prairies they were far less abundant being present in only one-third of them. They ranked in fourth place in 18 per cent and first in only 4 per cent.

Psoralea floribunda Nutt. is a legume of wide but irregular distribution in upland prairies (Figs. 10 and 11). It seldom occurs in low, wet soil. Although found in only 38 per cent of the high prairies, it ranked as a leading society in 17 per cent of them. The more regular occurrence in greater numbers was found in the drier portions of the prairie region. This plant is sometimes called "wild alfalfa" and indeed where the stand is thickest the prairie appears at a distance like an old, partially deteriorated field of alfalfa.

The individual plants vary greatly in size; the seedlings evidently requiring two or three years to reach maturity and to blossom. Usually there are 1 to 4 stems per plant, frequently 8 to 15, but sometimes more than 50. The stems are coarse and woody near the base where they mostly have a diameter of 3 to 8 mm. They appear above ground in April, and late in May are 12 to 15 inches tall. The bases of the stems are bare to a height of 4 to 6 inches and the leaves and flower buds are rather densely aggregated near the tops of the stems. When fully developed the tallest plants may reach a height of 2.5 to 3 feet. The stems of mature plants are usually leafless and unbranched to a height of 8 to 10 inches, but the tops branch profusely and spread widely. Thus a single large plant with a basal area of 25 square inches may have a bushy top approximately 3 to 4 feet in diameter. An average spread of tops is about 18 by 18 inches. However, because of the small expanse of foliage, together with the fact that the individuals are rarely spaced thickly enough to form a continuous upper story, even locally, they do not cast sufficient shade to affect materially the grasses. Exceptionally, plants have many small stems and tops so dense that bluegrass alone thrives beneath them.

The stems often spread 4 to 6 inches in the soil from the root-crown before becoming erect, so that unless they are pulled up one can not tell whether or not he is dealing with an individual. In fairly thick stands 6 to 12 plants and 8 to 40 stems occur per square meter but where best developed there may be several times these numbers.

The small blue flowers of this estival bloomer begin to appear about the first of June and soon are sufficiently numerous to warrant the specific name floribunda. A single large plant with 13 stems had over 800 flower clusters and nearly 20,000 individual flowers. Where the species is at all abundant it gives a distinct tone to the landscape. Fruits begin to appear in a few weeks but they are much fewer than the flowers. During late July and August the whole plant dries as the stem naturally develops an abscission layer at or near the soil surface. The wind breaks the stem and blows the whole plant before it as a tumble weed over the tops of the grasses. They mostly find lodgement in "draws" and low places where they sometimes accumulate into drifts several feet in depth.

The new growth springs from the crown of the pronounced taproot which is frequently more than an inch thick. Since it penetrates a foot or more before branching, little absorption occurs in the upper layers of soil. The large branches of this generalized root system spread widely, and, like the taproot, penetrate deeply, to 6 to 10 feet. To this depth the soil is enriched by the nitrogen-fixing bacterial nodules, and finally by the decay of the roots themselves.

Psoralea esculenta Pursh is a rather widely spread legume of upland prairies, practically never occurring on low ground. Although it was found

in half of the high prairies its highest ranking was third class (9 per cent) and it was found nearly five times more often as a species of fourth or fifth rank. Thus it is fairly abundant only as isolated individuals. From the deeply penetrating, "tuberous" taproot, the shoots renew growth in early spring. Much farinaceous and glutinous food is stored in the swollen portion of the root, which in mature plants is often almost spherical in shape and 2 inches in diameter.

During the first week in May, when the stem is 4 to 6 inches tall and the leaves are just unfolding, the large inflorescences are already prominent (Fig. 16). The plant is ordinarily not more than 20 inches tall but the top usually has 3 to 5 branches. During June, the spreading flower stalks and leaves occupy an area of 8 to 12 inches in width, but the leaves are so scattered that their shade has practically no effect upon the grasses beneath them. The small blue flowers are not very conspicuous. Soon after the first of July the stems break near the soil by a natural process of abscission and the seeds are scattered as the dry plant is blown about by the wind. It is the earliest of the psoraleas to be thus distributed.

This "prairie apple" or "prairie turnip" is said to have been one of the food plants of greatest importance obtained from the prairie by the Indians. After the roots were peeled they were eaten either raw or after cooking. "Large quantities were dug in June and early July to peel and dry for the winter food supply. The peeled roots were braided in long strips by the tapering ends, as strings of garlic are braided by the tops" (Gilmore, 1919). The enlargement of the root is several inches below the surface of the soil and harvesting it was no easy task.

The wild rose, *Rosa arkansana* S. Wats. (*R. suffulta* Greene), is a characteristic and widely distributed half-shrub of both upland and lowland (Fig. 75). In high prairies it was represented in all but 26 per cent with a ranking in first to fifth class of 13, 8, 27, and 26 per cent. It was absent in 65 per cent of the lowlands, but ranked first or second in 36 per cent of these areas. In the drier prairies westward, it is more or less confined to low ground but with increasing rainfall it is scattered over the hills as well.

In unmowed prairie this species becomes a tall shrub 2 to 3 feet high, forming dense bushes and casting much shade. Here the woody stems are 0.2 to 0.5 inch thick. But in the mowed grasslands it must start anew each year and is consequently less woody and somewhat smaller—about 18 to 20 inches tall on lower midslopes. Often the stems are spaced singly on the extensive rhizomes and there are rarely more than 3 to 5 in one clump. The leaves usually overtop the upland grasses, at least in part. The stems are very leafy (although by midsummer in dry years there may be few remaining to a height of 6 to 8 inches) and where the society is dense they shade the grasses to a considerable degree. Even in big bluestem prairies the tops

FIG. 75. The prairie rose, *Rosa arkansana*. A single plant is shown at the right; and two stems from larger plants. Photo. June 26.

FIG. 76. *Sisyrinchium angustifolium* (blue-eyed grass) taken early in May.

reach the general level of the grasses at 2 or more feet and here the shade enduring leaves are abundant to the base of the stem. It rarely occurs in wet places.

Growth is renewed in April and about June 1 the large pink buds unfold into the wonderful, white and pink tinted blossoms. These add beauty to the prairie well into July and later are replaced by an abundance of the pretty reddish "rose-hips" which are so prominent in autumn.

The plant spreads widely underground at a depth of 8 to 18 inches. The taproot may reach a depth of more than 20 feet. It is not well fitted for absorption in the surface soil but functions mostly far beyond the root-levels of the grasses.

Salix humilis Marsh., the prairie willow, was found in only 8 per cent of the upland prairies. But in a few cases it was so abundant that the grasses were nearly crowded out by the shade. The clumps are 2 to 6 feet in diameter and where thickest occupy one-fifth to one-fourth or even more of the surface of the soil. There is little or no grass under them except perhaps a thin sprinkling of bluegrass on the margins. By midsummer these leafy shrubs reach a height of 2 to 3 feet. Annual mowing undoubtedly hinders their full development.

Senecio plattensis Nutt. is a perennial species of wide distribution but usually of no great abundance nor importance. It is most frequently found in the prairies westward. It was found in 26 per cent of the uplands but seldom ranked higher than a society of the third class. The species was less abundant on lowlands (occurring in 15 per cent) where it had a similar distribution. It is a vernal bloomer, vegetative growth starting in March. During May its yellow flowers, usually in clusters of 3 to 12, are held aloft above the grasses on a stem only scantily clothed with leaves. Nor are the basal leaves, which are of variable pattern and often reddish beneath, abundant. This prairie ragwort occurs as isolated individuals, more often as very scattered societies, but sometimes, especially on lowlands, in compact, extensive ones with 10 to 20 plants per square meter. After the fruits have blown from the cottony ball into which the flowers have ripened, the whole plant dries. The basal leaves, or at least some of them, alone endure throughout the summer.

Sisyrinchium angustifolium Mill. and *S. campestre* Bickn. are low, slender perennials with fibrous roots and grass-like leaves. They occur as small tufts of many or isolated stems among the grasses. Large tufts often contain 30 to 40 spathes with 2 to 7 buds or flowers on each. Usually only 2 flowers are unfolded at one time on any one stem. The white or purplish tinged flowers of these "blue-eyed grasses" are conspicuous late in April or early in May (Fig. 76). They are held several inches above the old stubble of the last year's grasses. In June the spathes have elongated farther and hold the

small, globular, 3-angled capsules in a favorable position for the distribution of the seed.

The plants are too small to be of much importance unless they occur in great abundance. Sometimes there are as many as 15 bunches per square meter. The preference for uplands is shown by their absence in 78 per cent of the low prairies but only 49 per cent of the higher ones. In the former, they ranked first in 4 per cent and second in 12, but reached their greatest abundance (24 and 11 per cent) in third and fourth places.

Solidago rigida L., the stiff, flat-topped goldenrod, constitutes a serotinal society throughout the prairie. Except under severe competition, it produces vigorous clusters, the dense basal mat often persisting throughout mild winters. In fact where the grasses are continuously handicapped as in grazing, it increases enormously, mostly by rhizome propagation, and often becomes a real dominant. It is consequently a reliable indicator of overgrazing. But although of wide distribution in both lowland and upland prairies (being in 57 and 74 per cent respectively) it ranked first, second, or third in only 26 per cent of the lowlands but in 48 per cent of the uplands.

Renewing growth early in spring and drawing upon its accumulated food supplies, this goldenrod is often 6 inches tall early in May, the stiff unbranched stems becoming prominent. These may occur singly but are more often in groups of 2 to 8 or more. Because of the large, broad leaves even a small clump casts considerable shade and where the stems are at all closely spaced the immediate area is usually free from grasses. Flowering begins after the middle of July, when the plant has reached a height of 1.5 to about 3.5 feet (Fig. 81). In drier grasslands it is confined to low ground but in more moist ones occurs also on upper slopes and hilltops.

This goldenrod possesses roots that are fibrous, very numerous and widely spreading, and they penetrate deeply. In these respects they resemble those of many grasses, but are much less branched. The roots extend to a depth of at least 5 feet and always compete more or less severely with the grasses for water and nutrients.

Solidago rigidiuscula (T. & G.) Porter is a slender, showy goldenrod with mostly unbranched stems ranging in height from 2 to 3.5 feet. It may occur as a single stemmed plant or a few stems grouped together, but well established clumps 4 to 8 inches in basal diameter are not infrequent (Fig. 78). By the first week in May this perennial is usually 4 to 8 inches tall and the stems are very leafy. Areas with 25 plants per square meter are to be found but more often the plants are rather widely scattered. Where the stems are grouped in numbers the other vegetation is almost entirely shaded out. This species is typical of uplands occurring in about one-half of them. In a few cases it formed societies of the first or second class but nearly always held a rank of third or fourth place. It was found in 12 per cent

FIG. 77. *Steironema ciliatum* from an understory to *Andropogon furcatus*, July 15.

FIG. 78. A large *Solidago rigidiuscula* in late bloom. Grasses have been removed in foreground. Photo. Sept. 27.

of the low prairies, ranking first in 3 per cent but twice as often in fourth or fifth place.

The beautiful golden flowers begin to appear late in August and the height of blooming is reached in September. Even after the flowers are gone, the yellow involucres, held about 2 feet above the surface of the soil, make the plants conspicuous.

Viola pedatifida G. Don, the prairie or crowfoot violet, arises early in spring from a short vertical rootstock and is characterized by palmately, deeply segmented leaves. The violet flowers from this modest little plant, which is only 2 to 7 inches tall, appear late in April but are more abundant in May. Plants vary in size from those with 2 or 3 leaves and 1 or 2 flowers to others with a cluster of 30 leaves and 18 or more flowers. Usually they are found rather widely separated, but sometimes they are so abundant as to give the local landscape a violet tone. The capsules from the cleistogamous flowers are light gray or yellowish when ripe. Many of the leaves disappear after midsummer.

Certain species in the remainder of the list are of fairly constant occurrence although they are usually found in small numbers or for other reasons are relatively of low ecological rank. Among these may be mentioned *Comandra umbellata* (L.) Nutt., *Drymocallis agrimonioides* (Pursh) Rydb., and *Physalis lanceolata* Michx. Other plants belonging to this group are the several species of Lithospermum, *Hedeoma hispida* Pursh, *Aster sericeus* Vent., *Meriolix serrulata* (Nutt.) Walp., *Gentiana puberula* Michx., and species of Acerates.

Space does not permit a discussion of their autecology but it should be emphasized that each of these is a characteristic species of the prairie. The downy gentian, for example, a small plant growing within the grass cover, occurs usually as widely separated plants; often only a single specimen was found. It is entirely possible that it and similar isolated species were overlooked notwithstanding careful study. But while its distribution is of interest, the species is of little importance in the structure of the vegetation. Some species of Acerates are often met in the prairie standing just above the sea of grasses but the plants are nearly always so few that they are impressive only because of their infrequent occurrence. The silvery-leaved *Aster sericeus* and *Drymocallis agrimonioides* have a somewhat similar distribution. Several species of the bell-like flowered and bladdery fruited Physalis occur from time to time, being almost obscured by the grasses. Several species, although often found singly, are sometimes quite gregarious in habit. Such are Comandra, Lithospermum, Hedeoma, and Meriolix. But when all are taken together their importance as components of the plant cover is not great.

SPECIES MORE CHARACTERISTIC OF LOWLANDS

A group of 67 of the most important species of lowlands is given in Table 16. Their sequence of arrangement is based on the order of their importance as determined by their occurrence as societies of first and second rank. The great importance of *Galium tinctorium*, for example, is shown by its occurring as a society of the first class in 36 per cent of the low prairies and being of second rank in 16 per cent more.

TABLE 16. *Distribution and relative importance of the chief forbs of lowland prairie and their occurrence in upland. The numbers under columns 1, 2, 3, etc., give their percentage occurrence as a society of the first, second, etc., class, and the numbers under column 0 the per cent of prairies in which the species did not occur.*

Species	Low Prairie						High Prairie					
	1	2	3	4	5	0	1	2	3	4	5	0
Galium tinctorium	36	16	18	4	0	26	0	0	2	1	3	94
Fragaria virginiana	30	17	5	20	0	28	5	7	15	12	6	55
Steironema ciliatum	20	25	29	9	17	0	0	0	1	2	1	96
Aster salicifolius	27	17	25	12	10	9	0	0	1	2	0	97
Anemone canadensis	27	17	6	11	2	37	0	0	4	2	0	94
Solidago altissima	28	15	29	14	0	14	2	3	4	9	9	73
Silphium laciniatum	22	18	11	4	11	34	12	3	10	10	10	55
Phlox pilosa	27	13	0	2	2	56	9	13	4	4	1	69
Silphium integrifolium	15	11	15	13	13	33	3	5	11	8	9	64
Helianthus grosseserratus	22	11	21	22	6	18	0	1	3	6	5	85
Liatris pycnostachya	29	2	9	14	2	44	6	3	6	7	5	73
Equisetum laevigatum	13	15	18	13	4	37	5	7	10	11	4	63
Zizia aurea	19	9	7	9	5	51	3	0	3	5	5	84
Teucrium canadense	14	9	29	20	11	17	0	0	0	4	3	93
Apocynum sibiricum	16	7	13	32	14	18	3	2	9	2	10	74
Viola papilionacea	14	6	11	23	6	40	0	2	1	3	5	89
Glycyrrhiza lepidota	9	9	25	8	6	43	0	1	2	9	3	85
Pycnanthemum virginianum and P. flexuosum	16	2	0	2	0	80	0	0	2	4	0	94
Cicuta maculata	14	2	14	24	8	38	0	0	0	0	0	100
Leptandra virginica	10	5	18	0	2	65	0	0	3	3	1	93
Asclepias verticillata	6	9	17	25	20	23	0	1	5	5	10	71
Asclepias sullivantii	11	4	9	20	18	38	0	0	2	4	4	90
Equisetum arvense	10	3	3	11	5	68	0	1	3	3	1	92
Lythrum alatum	10	2	10	12	2	64	0	0	0	2	0	98
Erigeron annuus	6	6	6	2	8	72	3	1	1	2	2	91
Vernonia fasciculata	3	8	20	20	15	34	0	0	0	1	3	96
Helianthus tuberosus	0	11	8	13	5	63	0	0	0	0	4	96
Asclepias incarnata	0	11	0	21	4	64	0	0	0	0	0	100
Hypoxis hirsuta[9]						30						70
Heliopsis scabra	6	4	12	18	18	42	0	0	5	10	11	74
Thalictrum dasycarpum	2	7	4	20	11	56	0	0	1	1	3	95
Persicaria muhlenbergii	2	6	19	16	6	51	0	0	0	0	0	100
Rudbeckia hirta	3	5	16	8	0	68	8	2	3	4	1	82
Lepachys pinnata	3	5	6	3	6	77	1	0	3	6	2	88
Senecio aureus	8	0	3	5	0	84	1	1	0	1	2	95
Lycopus americanus	7	0	7	12	9	65	0	0	0	2	0	98
Silphium perfoliatum	2	5	5	14	11	63	0	0	1	1	0	98
Vernonia baldwini	2	4	18	20	6	40	1	4	6	28	10	51
Physalis heterophylla	3	3	11	3	20	60	0	0	7	9	13	71
Erigeron philadelphicus	3	3	0	8	8	78	0	0	0	2	1	97
Lobelia spicata	0	5	7	32	2	54	0	0	3	22	10	65

TABLE 16. *(Continued)*

Species	Low Prairie						High Prairie					
	1	2	3	4	5	0	1	2	3	4	5	0
Allium canadense	0	5	5	18	10	62	0	0	1	0	2	97
Helenium montanum	5	0	5	3	0	87	0	0	1	1	0	98
Oxalis stricta	2	2	20	11	13	52	0	1	2	9	13	75
Rhus toxicodendron	3	0	17	11	6	63	0	1	6	19	5	69
Helianthus maximiliani	0	3	12	12	9	64	0	1	1	3	1	94
Cirsium undulatum	3	0	9	23	11	54	0	1	1	15	18	65
Mesadenia tuberosa	3	0	8	16	19	54	0	1	2	4	18	75
Meibomia illinoensis	3	0	5	12	10	70	0	0	1	0	1	98
Antennaria plantaginifolia	3	0	0	3	0	94	0	1	2	2	1	94
Physalis virginiana	0	3	5	8	16	68	0	1	4	4	11	80
Astragalus canadensis	0	3	5	5	16	71	0	0	2	8	11	79
Amphicarpa pitcheri	0	3	3	5	10	79	0	1	0	1	0	98
Gaura (all species)	0	3	3	3	11	80	0	0	1	6	8	85
Oxalis violacea	0	3	3	5	3	86	2	1	1	3	2	91
Artemisia ludoviciana	0	3	0	3	3	91	0	0	1	3	3	93
Lathyrus palustris	2	0	2	6	6	84	0	0	4	4	4	88
Vicia americana	0	0	8	8	5	79	0	0	1	2	6	91
Monarda fistulosa	0	0	7	10	8	75	0	0	0	3	4	93
Solidago canadensis	0	0	5	10	12	73	0	0	8	11	3	78
Tradescantia bracteata	0	0	3	8	8	81	0	0	1	2	5	92
Oenothera biennis	0	0	0	11	24	65	0	0	1	4	13	82
Chamaecrista fasciculata	0	0	0	6	3	91	0	0	1	1	4	94
Allionia nyctaginea	0	0	0	3	11	86	0	0	0	0	5	95
Lilium canadense	0	0	0	0	17	83	0	0	0	1	6	93
Potentilla monspeliensis	0	0	0	0	11	89	0	0	0	3	3	94
Lithospermum arvense	0	0	0	0	11	89	0	0	0	5	3	92

* After the cessation of blooming, Hypoxis is not readily distinguishable from the grasses, hence it was not ranked into the several classes of societies as were other forbs.

The ecology of the seven most important species is given, after which the other species that are described are considered in their alphabetical order by genera.

GALIUM TINCTORIUM

The stiff marsh bedstraw, *Galium tinctorium* L., is a small perennial herb with 4-angled erect stems. These arise from the abundant, rather shallow underground parts. The plant is branched and leafy to near the base; the branches are mostly solitary and the leaves small so that all are fairly well lighted even where, as usual, the plants are densely aggregated. This arrangement is almost imperative since this Galium nearly always forms a dense understory in wet grasslands and sloughs (Fig. 79). The height attained seldom exceeds 10 to 18 inches but the plants start early and the stems are nearly erect. Westward it rarely migrates far into low prairie proper but associates mostly with Spartina, *Agrostis palustris,* and various carices. But under a higher precipitation it is found in the less hydric habitats such as lower slopes and sometimes on hilltops, where it has migrated from ravines. Thus this species was found in 6 per cent of the uplands and in 74 per cent of the low prairies. In the latter it formed societies of the first class in 36

per cent and of the second and third rank in 16 and 18 per cent, respectively.

The tiny, white, terminal flowers are present from May until July when they are usually replaced by the small, smooth, shining green fruits.

FRAGARIA VIRGINIANA

Fragaria virginiana Duchesne is a widely distributed species, occurring throughout the whole of the region studied. In the more xeric western part it occurs only in the lowlands and along ravines, but southeastward, with increasing rainfall, it is found on uplands as well. In many prairies it is rather uniformly distributed even over hilly land. It was found in nearly half of the high prairies, and ranked first, second, and third in 5, 7, and 15 per cent of these grasslands. On low prairie it was absent from a few more than one-fourth of the areas but here it ranked as a society of the first class in 30 per cent of the fields studied. It is thus a good indicator of moist soil. The root system, like that of the cultivated varieties, is probably less extensive and shallower than that of most prairie forbs. The strawberry is not only found as an understory where there is a dense stand of big bluestem—although it develops better where this grass is thinner—but also occurs in wetter communities (Fig. 80). It is often found in sloughs with Spartina or associated with *Tripsacum dactyloides*. Frequently the plants are densely aggregated.

In early spring, extensive societies are common in ravines and in low prairies. At first the plants are only one to two inches tall and the leaves are mostly spread near the soil surface, but with the growth of the grasses they take on a more erect position. In uplands where the species is less densely aggregated and the grasses shorter, they rarely exceed 5 to 8 inches in height. But where the shade is pronounced a height of 12 to 14 inches is attained.

Propagation, as in cultivated varieties, is mostly by runners rather than by the short, thick, shallow rhizomes. These almost leafless stems reach a length of two or more feet late in May.

Flowering begins early, often before the new leaves are more than half grown, and reaches its maximum about the middle of May. The pretty, white flowers are about 2 to 3 cm. in diameter and very conspicuous. They often occur in dense clusters of 12 or more flowers and fruits per plant. The large clusters of bright red, delicious fruits ripen during June. Upon the advent of severe drought the leaves roll upward until the edges almost touch; otherwise this forb remains green until frost.

STEIRONEMA CILIATUM

The fringed loosestrife, *Steironema ciliatum* (L.) Raf., is one of the most important forbs of wet areas. It is found in almost every wet area and forms very extensive societies. This perennial herb renews growth early in spring and by the middle of May is 4 to 12 and occasionally 18 inches high.

Mature plants vary from 1 to over 3.5 feet in height (Fig. 77). It is a gregarious species and grows in dense stands due to running, underground

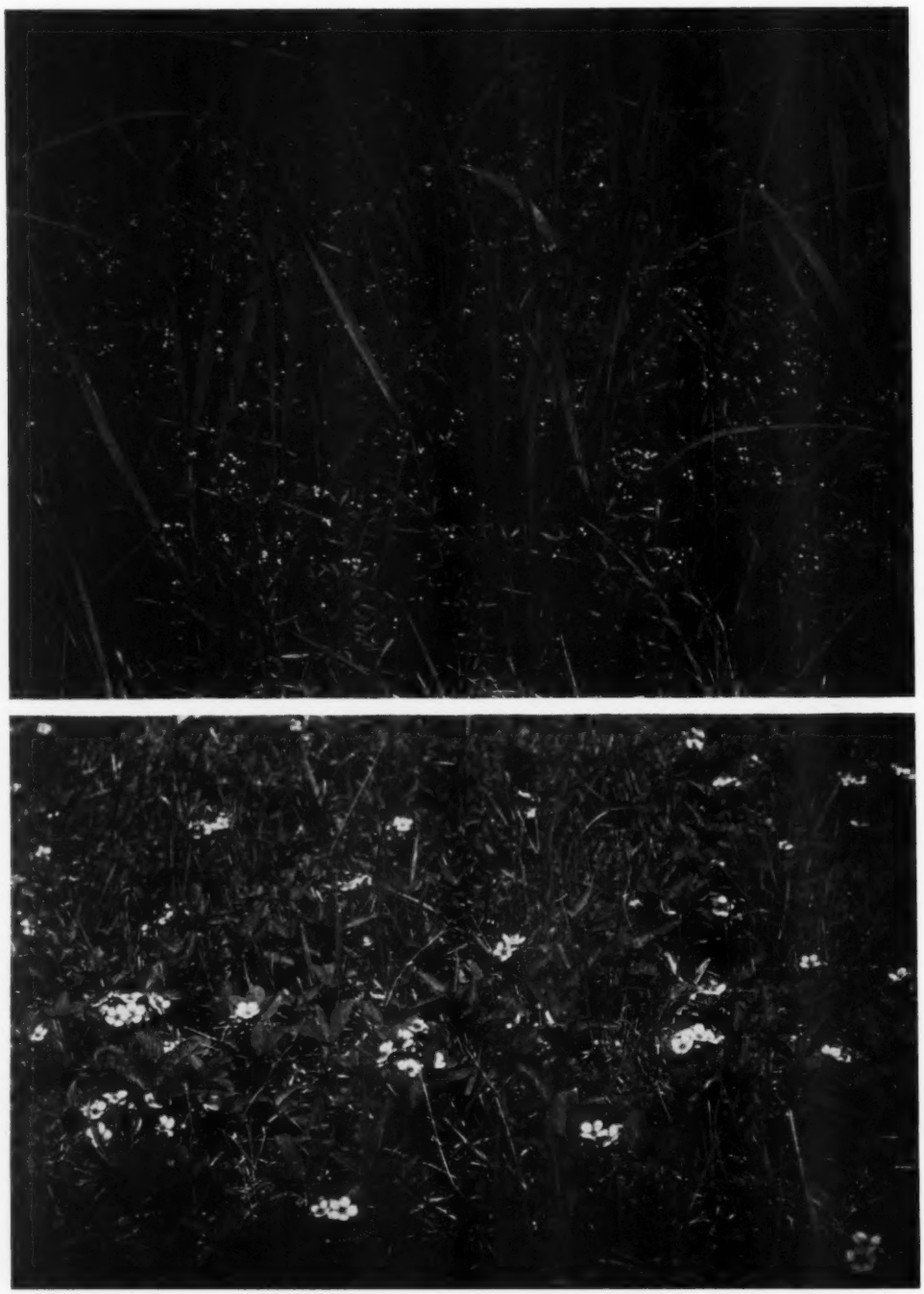

FIG. 79. Layer of *Galium tinctorium* under big bluestem. Wisner, Nebr., June 10.

FIG. 80. Society of *Fragaria virginiana* on low ground, Hamburg, Ia., May 6.

branches an inch or two below the soil surface. Sometimes it alone constitutes half or more of the plant cover. It is very tolerant of shade, and the unbranched, erect stems are usually leafy to the base, at least until midsummer. The pairs of opposite leaves are widely spaced and unless the plants are very closely crowded they do not shade each other to a great degree. But the best development is reached where the grasses, etc., are less dense or almost absent. The pretty yellow flowers, whether axillary or terminal, are held conspicuously above the foliage by the peduncles. Notwithstanding much shading, the plants remain green until frost.

Eastward this species is not only an important constituent of the wetter low prairies proper but also occasionally migrates from ravines well into the little bluestem sod. Well formed patches of plants 20 inches tall and in full bloom have been seen. Its wide distribution is shown by its presence in every low prairie (including ravines) studied. In 20 per cent it ranked as a society of the first class and held second and third rank in 25 and 29 per cent, respectively.

ASTER SALICIFOLIUS

Aster salicifolius Lam. (including *A. paniculatus* Lam. in part) is a tall perennial that occurs rather abundantly on the better watered lowlands or the margins of ravines at the foot of steep, dry slopes where run-in water moistens the soil. In fact, it was absent from only 9 per cent of the lowlands, though frequently ranking in fourth or fifth place. As a society of the first rank it was found in 27 per cent, and of the second and third, in 17 and 25 per cent of the low prairies. It grows well also in the wetter types of grasslands, very frequently occurring with Spartina. Growth begins early in spring and by the middle of June the plants are usually about 2.5 feet high in moderately moist soil. Where it is wetter this stage in development is reached by the end of May. Later the bases of the woody stems defoliate and in September the much branched tops are covered with a wealth of flowers. The plants are 3.5 to 7 feet high.

ANEMONE CANADENSIS

Anemone canadensis L. is a widely distributed, very conspicuous, and often important forb of low prairies. It is best represented in the wettest big bluestem areas where the grasses are not too dense and especially in the other wetter types of prairies and sloughs. Here, due to its method of propagating by rhizomes, it often forms dense more or less circular "islands" a few to many feet in diameter. It was found in all but 37 per cent of the low prairies, and held first and second rank in 27 and 17 per cent, respectively. Anemone is also found in moist soil of nearly level, poorly drained uplands, being associated with big bluestem, slough grass, or tall panic grass, but sometimes with sedges, in the wetter parts. In the less favorable sites it

is often represented by scattered individuals but where best developed it has almost exclusive possession (Fig. 20).

In drier areas and where there is less competition for light, this species is only about 8 inches tall, but in lowlands, when considerably shaded, a height of 12 to over 18 inches is attained. In such places the first cauline leaves are 12 inches above the soil and the petioles of the few basal leaves are 4 to 6 inches long. Thus the foliage is brought into the light. Indeed the leaves are often so thickly placed that they almost obscure the soil. They begin to appear in April and remain green until late in the fall.

The abundant, large, white flowers unfold during the latter half of May and for several weeks areas of low prairie and broad, flat swales in uplands are veritable flower gardens. Hundreds of flowers 1.5 to 2 inches in diameter are held by long peduncles well above the level of the grasses.

SOLIDAGO ALTISSIMA

Solidago altissima L., the tall goldenrod, is a common and conspicuous species of low prairies. Here it was found in all but 14 per cent, and as a society of the first or second class in 43 per cent. It occurred in 27 per cent of upland prairies, being found only in the less xeric ones, and rarely in abundance. In fact, it is even more characteristic of the wetter types of grassland than it is of the big bluestem areas.

This coarse perennial, like most lowland species, begins growth in early spring and develops with marked rapidity. Early in May it is 7 to 12 inches tall and possesses about 15 linear leaves. Until the plants reach a height of a foot or more, they have a definitely nodding top resulting from unequal lateral growth. The unbranched stems are 1.5 to 2 feet high by the middle of June, and mature plants vary from 3 to 6 feet or more in height (Fig. 83). Thus at all times this species is well above the general level of the big bluestem. Where the grass is dense, the stem of the goldenrod is defoliated by August to a height of 1 to 2 feet. Still the photosynthetic area is great since the plant is very leafy.

This goldenrod is usually most abundant in ravines and at the borders of the grasslands. In the prairie proper, however, it is sometimes represented by 50 or more stems to the square meter. Even then there is little competition with the grasses for light since most of the leaves among the grasses have fallen. In the ravines such dense stands occur that the very tolerant *Poa pratensis* alone of all the grasses can withstand the shading. In the more moist prairies of the southeast this species occurs as an important forb of uplands and sometimes on hilltops.

The tall goldenrod is an autumnal bloomer, the large golden thyrsus appearing late in August or early in September. Seeds are produced in quantities and vegetative propagation is by means of rhizomes.

SILPHIUM LACINIATUM

The compass plant, *Silphium laciniatum* L., is a very coarse, tall composite characteristic of low prairies and wet ravines in the north and west, but also occurs regularly on uplands including hilltops in the better watered areas south and east. It varies greatly in height (3.5 to 10 feet) and number of stems, according to age and the supply of water. A single large clump frequently has 100 to 150 coarse, basal leaves arising from an area 6 to 9 inches in diameter. It has a spread at or above the grass level of 3 to 5 feet. The

FIG. 81. Three stems of *Solidago rigida* on July 25. Later the lower flowering branches elongate to form a flat-topped inflorescence.
FIG. 82. *Silphium laciniatum* about 5 feet tall on July 24.
FIG. 83. *Solidago altissima* on Sept. 1, extending about 3 feet above the general level of the big bluestem.

coarse stems are 0.5 to 1 inch in diameter, and individual leaves 18 to 20 inches long and 14 inches wide. The shade is dense and the prairie grasses are usually replaced on the periphery of the clumps by the more tolerant bluegrass. Upon the removal of Silphium, a noticeably large, bare area frequently remains, or it may be thinly populated with bluegrass. Thus an abundance of the compass plant greatly reduces the yield of the grasses. In drier areas the largest bunches usually do not exceed 2.5 feet in diameter but in moist soil the width may reach 5 feet. In areas that are occasionally grazed or flooded the plants may become very abundant, there being as many as 60 to 75 seedlings or 5 to 6 older plants or clumps per square meter. They thrive in places dominated by tall panic grass or wild rye and may also be found in relict areas of slough grass. The vertical leaves, especially of

younger plants, have the orientation of a compass, the sides receiving the morning and afternoon sun.

This species well illustrates the rapid development of perennials with a large accumulation of food. Starting late in April, it reaches a height of about 2 feet by the first of June. By the last of this month the large, coarse, yellow flowers begin to appear. These clothe the upper 2 or 3 feet of the stem as shown in Figure 82. Blossoming continues for several weeks and the plant remains green until frost. From the involucres and upper parts of the stem much gummy material exudes and solidifies. The Indians and pioneers, especially the children, gathered it for chewing gum.

Silphium has a large, fleshy, deep taproot. The diameter just below the multicipital crown varies from 1 to 3 inches. The main root descends almost vertically, tapering gradually, to a depth of 9 to 14 feet. It is poorly fitted for absorption in the surface two feet of soil but is fairly well branched and penetrates a large volume of subsoil much of which is not occupied by the roots of the dominant grasses.

Other Species

Apocynum sibiricum Jacq. (*A. hypericifolium* Ait.), the clasping-leaved dogbane, is an important forb, mostly of low moist soil, throughout the whole region. It occurred on about one-fourth of the upland prairies, also, where its ranking was usually as a society of the third to fifth class. On low ground it was found in all but 18 per cent of the prairies. Here it ranked in first, second, and third places in 16, 7, and 13 per cent of them, respectively.

This glabrous, pale green perennial renews growth early each year from strong underground parts. It is usually 8 to 10 inches tall before other than scale-like leaves appear. It ultimately attains a height of 1.5 to more than 3 feet (Fig. 84). The stout stem is usually bare by midsummer to a height of 6 to 10 inches but otherwise clothed with sessile, opposite leaves. These are 1 to 4 inches long, 0.5 to 1.5 inches wide, and rather closely spaced. Hence the total spread of the foliage is 6 to 8 inches. The upper one-half to two-thirds of the plant, moreover, is furnished with several ascending branches so that the total spread of tops is usually a foot or more. Under competition with the grasses, the stems are mostly singly spaced but connected to others within a distance of a few inches. Thus sometimes 15 to 20 plants may occur per square meter, although this is exceptional. Their shading effect upon the grasses is little. From late June until August the reddish stems and many white-flowered cymes show conspicuously among the grasses, mostly standing above their general level. In fact, they are quite as conspicuous after the long slender follicles replace the flowers in late summer or fall. The silky seeds are widely distributed by the wind.

Asclepias verticillata L. is a long-lived perennial with a deep, fascicled root. The very narrowly linear leaves occur in whorls upon the slender, erect

FIG. 84. *Apocynum sibiricum* about 3 feet tall and in full bloom on July 5.
FIG. 85. *Asclepias incarnata* from area of slough grass. Stems defoliated to height of 2.5 feet. Photo. July 30.

stems; hence the name, whorled milkweed. A single plant has practically no effect upon the grasses. Usually, however, the plants occur in considerable abundance, although spaced a few inches apart. This is a result of the rhizome habit. Even then the total shading effect is not great. The greenish white umbels are especially conspicuous during July and August and the erect, narrow, spindle-shaped pods in late summer and autumn. It was a component species in 29 per cent of the uplands, but usually of third or lower ranking. In low prairies it was found in all but 23 per cent. Here it occurred as a society of the first class in 6 per cent; as second and third in 9 and 17 per cent; but rated highest (25 and 20 per cent) in fourth and fifth places. This plant is poisonous to stock.

Asclepias sullivantii Engelm. is a thick stemmed, perennial milkweed arising from a thick rhizome. It is leafy to the top. The small basal leaves occur first at a height of about 8 inches and later these are shed. The stems extend well above the tall grasses before the leaves unfold. The plants, which are 3 to 4 feet tall, nearly always occur as one or a few individuals and seem to have little harmful effect upon the grasses. Where thickest, they rarely exceed 4 or 5 to the square meter. This species is found sparingly on lower slopes or the edges of ravines in the less xeric uplands and is typical of well watered low prairies. In fact it is often more abundant in even wetter situations such as Spartina sloughs. It ranked as a first class society in 11 per cent of lowlands but in fourth or fifth place in 38 per cent. It was present in nearly two-thirds of such areas.

The large terminal or upper axillary umbels are many flowered and very showy with their delicate shades of pink and rose. These appear late in June (Fig. 7). They are, however, scarcely more conspicuous than the large, erect follicles or "pods" that replace them as the season advances.

Asclepias incarnata L. is a tall, coarse, and usually single-stemmed, perennial plant. It arises from a base that is furnished with several score of fleshy, fibrous roots 2 to 4 mm. in diameter. The stem is often 0.5 inch in basal diameter, defoliated to a height of 1 to 2 feet by midsummer, and the upper part frequently furnished with a branch at every node. Thus this swamp milkweed, which is 2 to 5 feet tall, has a rather bushy top that usually exceeds a foot in diameter. The slender glabrous stem is clothed above (and earlier to the base) with numerous, lanceolate leaves 3 to 6 inches long (Fig. 85). It is intolerant of shade and persists only because it extends well into the light above the tall coarse grasses. Blossoming occurs in July and August. The numerous, corymbed, many-flowered umbels consist of red, rose-purple, or sometimes white flowers, which in mass are conspicuous. Later they are replaced by numerous erect follicles 2 to over 3 inches long.

This species occurred in about one-third of the low prairies and ranked as a society of the second class (but never first) in 11 per cent of them. It is indicative of low, wet soil.

Astragalus canadensis L. (*A. carolinianus* L.) is a much larger plant than *A. crassicarpus* but of more limited distribution and of far less importance. It was found in only 21 per cent of upland prairies but in 29 per cent of the lowlands. Typically the plants are widely scattered and few, preferring lower slopes. This coarse legume reaches a height of 3 to 4 feet. On a low prairie in Minnesota, flooding had thrown the balance in favor of this milk vetch and it overran the big bluestem meadow. The woody stemmed plants formed brush-like thickets; 126 stems were counted in a single square meter. They made the area worthless for hay.

The water or spotted hemlock, *Cicuta maculata* L., is a stout, erect, much branched, perennial herb that is found only in moist or wet soil. It varies in height from 3 to 6 feet. The base of the great, hollow, glabrous stem is frequently an inch thick. It is often marked with purple lines. The general level of the blades of the bi- or tripinnate, long petioled, basal leaves usually varies between 16 and 32 inches. The petioles are mostly 1 foot to more than 2 feet long and the outline of the compound blade usually includes more than a square foot of area. The coarse leaves are fairly numerous (Fig. 86). Early in July when the lowland grasses are over two feet tall and the shade is dense, some of the basal leaves turn yellow and die, although the general leafy level is approximately that of the big bluestem. Some new leaf blades continue to unfold, however, after the petioles are 18 inches long. The stems are leafy to the top; the leaves rapidly decrease in size with an increase in height of the stem.

Water hemlock is supplied with several fleshy roots some of which may reach an inch in diameter. Like the stem, they possess a carrot-like odor. The plant is poisonous. From an abundance of stored food, the new growth develops early and rapidly. Full stature is reached and blossoming of the large umbels of tiny white flowers begins late in June.

This species was found in about two-thirds of the low prairies, often in soil wetter than that occupied by big bluestem. It ranked as a society of the

FIG. 86. Single *Cicuta maculata* 5 feet high on June 24. Note the great height of the foliage, which is at about the upper level of the grasses.

FIG. 87. *Helianthus grosseserratus* with base of stems (plants in sections) defoliated to a height of more than 2 feet. Photo. Sept. 20.

first class in 14 per cent of these areas but nearly three times as often in third or fourth place.

Equisetum laevigatum A. Br. is often an important species in both upland and lowland prairies. It was found in 37 per cent of the former and 63 of the latter. On upland it was a leading society in 5 per cent of the areas; on the lowland in 13 per cent. Its distribution throughout the other classes is rather uniform and fairly high.

The new plants appear from the rhizomes in April. Late in June a height of 2.5 to 3.5 feet is attained, and terminal cones are produced in abundance. Lower slopes, ravines, and other well watered areas are favorable sites for this rush-like perennial, but it is also found in rather dry places. Sometimes it forms alternes with the carices in low areas, constituting one-third or more of the local vegetation. One hundred twenty-five of the unbranched stems of this scouring rush per square meter are common in many grasslands; some-

times there are two to three times this number (Fig. 21). As many as 400 to 500 to the square meter have been counted in the Platte Valley where other vegetation was sparse. Where at all abundant, both the yield and quality of hay are reduced. The plants remain green until frost and sometimes over winter where well protected by the grasses. They contain large quantities of silica, hence the name "scouring rush." It and the following species were used by the Indians for polishing their bows, etc., much as we use sandpaper.

Equisetum arvense L. occurred in 32 per cent of the low prairies and ranked as a society of the first class in 10 per cent of them, but held a rank of fourth or fifth place in 16 per cent. It is rarely found on upland, but is important in the wetter types of grassland where it often forms a dense, more or less continuous understory 6 to 18 inches high. The unbranched, fertile shoots develop very early in spring from the tuberous rhizomes. After the spores are shed these disappear. The "horsetail" of late spring and summer is the tall, much-branched, sterile stem.

Glycyrrhiza lepidota Nutt., a wild licorice, is a legume that forms extensive patches on lower slopes where at least the deeper roots have contact with well moistened soil. It is always an indicator of well drained, rich, moist land. Frequently 20 to 50 plants occur in a square meter. They are found often as single-stemmed plants, more usually 2 to 5, but because of its underground habit they sometimes occur in fairly dense clusters. The rather leafy stems, which are often bare to a height of 10 inches, are 2 to 3.5 feet tall. They seem to exert little harmful effect upon the grasses. The flowers of June and July are much less conspicuous than the dark brown pods with their hooked prickles which reach maturity in August and September.

The much branched rhizomes are several feet long and the fleshy taproot is 0.5 inch to over 2 inches in diameter. The roots spread widely and reach far below the absorbing level of the big bluestem. Well branched roots are frequent even 8 to 12 feet or more below the soil surface.

This species was found in only 15 per cent of upland prairies where it ranked most frequently in fourth place. But in lowlands it occurred in 57 per cent and ranked first or second in 18 per cent. An even higher percentage (25) was attained as a society of the third class.

Helianthus grosseserratus Martens is a very tall, coarse, leafy, single-stemmed composite. It is mesic in habit and if found on moist uplands it is rarely abundant. The saw-tooth sunflower is abundant in draws where it forms dense stands and from which it migrates, especially during a series of wet years, several yards into the higher ground, the plants becoming dwarfed and widely spaced. It occurred in all but 18 per cent of the low prairies and was so abundant in 22 per cent as to form a society of the first class. Its ranking in third and fourth places was similar, thus showing the importance of this lowland plant.

Growth from the strong rhizomes and thick crown begins early in April

FIG. 88. Portion of society of *Helianthus tuberosus* near Glenwood, Ia., Sept. 1.

FIG. 89. *Hypoxis hirsuta* in low prairie at Holton, Kans., May 8.

and proceeds very rapidly. By the first of May a height of 10 to 15 inches is attained and the first of the long, coarsely serrate leaves reach nearly full size. Vegetative growth continues until August when a height of 6 to 9 feet is reached even where competition with the grasses is fairly severe. The stems become defoliated to a height of 2 or more feet (Fig. 87). But the abundant, large, remaining leaves form a distinct, upper, photosynthetic layer. Where the grasses are thick, however, the stems are usually not closely spaced. A thick growth of this species with stems only 2 to 4 inches apart is found usually only in ravines or semi-denuded areas such as flooded lands.

Just as the stature of this perennial is an excellent indicator of the prevailing water content, so too the number and size of flower heads varies according to the habitat. Usually they are numerous and fairly large. Like many of the other sunflowers, this one is an autumnal bloomer, a maximum showing of the large yellow flowers occurring in September.

Helianthus tuberosus L. is a lowland sunflower of minor importance. It was found in more than one-third of the lowlands but ranked in second or third place 11 and 8 times, respectively. This species is characteristic of borderlands between prairie and the shrubs and woodland along ravines and streams (Fig. 88). It thrives along draws or on lowland where the soil has been deposited by flooding, etc. It is not so tall as *H. grosseserratus;* the leaves much more nearly approach those of the cultivated *H. annuus* in shape; the heads are few and the ray flowers orange-yellow; where much disturbance has occurred, as along roadsides, their number and size are greatly increased. The storage organ consists of tubers, often of considerable size (an inch or more in diameter) and abundance. These were eaten by the plains' Indians either raw, boiled, or roasted. It appears that they depended upon the natural supply and never cultivated the plant (Gilmore, 1919).

Heliopsis scabra Dunal is a coarse composite that was found in small numbers in about one-fourth of the upland prairies but occurred in 58 per cent of those of lowlands. Its rank as a society of the first or second class, however, was in only 10 per cent. The rough oxeye has a stiff stem, branched somewhat above, and 2 to 4 feet tall, that is clothed with firm, scabrous, broad, opposite leaves 2 to 5 inches long. It is intolerant of shade and the stems are usually defoliated to a height of 10 to 14 inches by midsummer. Even where they occur in small groups, as is their habit, they have little retarding influence upon the growth of the grasses. The large orange-yellow flowers are numerous, often 5 to 12 per plant and much more abundant where this species occurs as a roadside weed. The plants are conspicuous and the blossoms show clearly above the level of the big bluestems or other grasses from July until fall.

Hypoxis hirsuta (L.) Coville, yellow star grass, is a small perennial about 4 inches high which develops early in spring from more or less globose corms. These vary from one-fourth to one-half inch in diameter and usually occur

at a shallow depth. This species is widely distributed, occurring at least sparingly in most of the low prairies and along ravines or moister hillsides on many of the uplands. Southeastward it occurs over the hilltops as well. It is often very abundant and conspicuous. Sometimes there are 8 to 12 plants in bloom to the square decimeter and even when fewer they give a distinct tone to the landscape (Fig. 89). The height of the plant increases with competition for light. In little bluestem prairies it is often only 2 to 4 inches tall, but upon entering areas dominated by slough grass or carices it stretches up to 8 to 10 inches. Blossoming is most abundant in May and early in June. When the flowers disappear the small capsules are not prominent nor are the grass-like leaves which are all basal.

Lepachys pinnata (Vent.) T. & G. is a tall composite of frequent occurrence especially in upland prairies in the eastern part of the area. It was found in less than one-fourth of the high prairies and ranked as a first or second class society in only 1 per cent. This coarse plant is about a foot high early in May and continuously overtops the grasses, reaching 3 to 5 feet when fully grown in July (Fig. 91). There are usually only a few stems (4 to 6) per plant where it competes with the prairie grasses, although the clumps are much larger where it grows along roadsides, where the supply of water and nutrients is greater. The species shows distinct ruderal tendencies. The large, 3- to 7-parted, long-petioled, radical leaves are often so abundant as to form a layer at a height varying from 10 to 18 inches. The leaves on the simple or branched stems, although 6 or more inches long, are usually smaller and the upper ones much smaller than the broad radical leaves. By midsummer the bases of the stems are usually defoliated to a height of 12 or more inches. The cauline foliage is not very dense and this species does not shade the grasses excessively although it is quite tolerant of shade.

The numerous, large gray or brownish oblong disks appear by the middle of July. Each is furnished with 4 to 10 drooping yellow rays 1 to 3 inches long. The flowers are held aloft on a long, nearly naked peduncle. They continue blossoming well into the autumnal aspect and are often a conspicuous and pleasing feature of the landscape.

Leptandra virginica (L.) Nutt. is a tall, stout, erect, perennial herb of low, moist ground. It resumes growth early in spring from strong, branched rhizomes that are only one inch to a few inches deep and furnished with an abundance of strong, fibrous roots. Development of the simple stems is rapid and a height of 2 to 7 feet is attained in late June or July. The leaves are mostly verticillate, each whorl consisting of 3 to 9, more or less lanceolate, sharply serrulate leaves, 3 to 6 inches long. The lowest whorls of leaves are smaller than are those midway on the stem. By midsummer the foliage is usually dead to a height of a foot or more. The stems are mostly numerous. They sometimes form open clusters but are often rather densely grouped.

Frequently the clumps are 2 or more feet in diameter. Culver's root competes with the grasses at all levels and since the leaves are numerous and somewhat closely spaced they often furnish much shade. Under dense clusters the ground is almost bare.

The stems elongate considerably after the inflorescence begins to appear in June (Fig. 90). There are usually several of the dense, spike-like racemes 3 to 9 inches long. The terminal one blossoms first and for several weeks

FIG. 90. *Leptandra virginica* in full bloom in low ground, August 3.
FIG. 91. *Lepachys pinnata* near Oakland, Ia., showing leaves after grasses have been removed and abundance of flowers on July 23.
FIG. 92. Small specimens of *Liatris pycnostachya* in fruit, Sept. 1 (cf. Fig. 72).

flowering continues. The fragrant, white flowers are so numerous as to be very conspicuous. The long, slender filaments carry the yellow anthers far beyond the corolla of this scrophulariaceous plant. Hence, the name Leptandra.

This species was found on moist uplands only in the area of highest rainfall. It occurred in about one-third of the low prairies (mostly eastward) where it ranked as a society of the first, second, or third class 10, 5, and 18 times respectively.

Liatris pycnostachya Michx. is the most mesic of the four common species of the genus (Fig. 92). It is characteristic of big bluestem areas and is rarely found in much drier or much wetter grassland types. Except very locally, it is confined to the areas of higher rainfall southward and eastward. Here it may occur on high ground, and even on hilltops where there is a considerable amount of big bluestem. While present in 56 per cent of low areas, it occurred in only about one-fourth of the uplands. It ranked first

in 29 and 6 per cent of these, respectively. On uplands, plants were usually too few for a high rating.

This blazing star varies in height from 3 to over 5 feet, attaining one-third of its stature by the first of June. The unbranched stems arise from a strong corm, 3 to 4 inches in diameter and well furnished with fibrous roots. They are variable in number, 5 to 8 being commonly found, but sometimes 15 or more. The basal leaves, while narrow, are very long and abundant, there are often 100 or more. Early in life they are almost vertical, but later spread widely. Thus the base of the clump may occupy a considerable area from which the grass is excluded. Two to 5 large plants and numerous smaller ones were found per square meter where they were most abundant (Fig. 110). Flowering begins late in July and, since the inflorescence is 10 to over 12 inches long, for several weeks the landscape is ablaze with purple.

Lycopus americanus Muhl., cut-leaved water hoarhound, was found to occur in 35 per cent of the lowlands. In a few cases (7 per cent) it ranked as a society of the first class, but occurred more often in fourth or fifth place. The stiff, erect stems, which are often branched, reach a height of only 1 to 2.5 feet and are consequently more or less concealed by the grasses. They are perennial by suckers and have strong underground parts. The deeply cut, opposite leaves are rather closely spaced; the plant when branched often forms a somewhat bushy growth and is leafy to the base. Its effect upon the grasses, however, is not great. Flowering occurs usually from July to October but the blossoms are small and add little to the aspects.

The wing-angled loosestrife, *Lythrum alatum* Pursh, occurred in approximately one-third of the low prairies and ranked as a society of the first or second class in 10 and 2 per cent, respectively (Fig. 93). This erect, glabrous, perennial herb reaches a height ranging from 1 to 4 feet. It is dark green in color and usually much branched throughout the upper part. The rather small, sessile leaves do not spread widely from the stem and they become bract-like on the upper part where the axillary branches constitute a bushy top often 4 to 8 inches or more in diameter. Hence individual or loosely grouped plants have very little effect upon either the basal or foliage cover. Often the rather heavy and somewhat woody underground parts give rise to great clusters of stems so that this species alone constitutes half of the vegetation over areas several yards in extent. It thrives in very wet soil and is frequently most abundant in areas of slough grass and alternes of red top, but also occurs in big bluestem prairies, especially southeastward. It avoids excessive competition for light by an early growth in spring and later by the defoliation of the base of the stem. The deep purple corollas scarcely exceed 1.2 cm. in width but the flowers are abundant and conspicuous from late June to August.

Mesadenia tuberosa (Nutt.) Britton is a coarse composite arising from a thick, tuberous root. The common name, Indian plantain, is well deserved

because of its large plantain-like leaves. These at first form a large rosette but are carried upward with the elongation of the angled and grooved stem (Fig. 9). This occurs during June, the large corymbose inflorescence of small whitish flowers attaining a height of 3 to 6 feet.

Although rarely occurring except as isolated individuals, yet on a few lowlands as many as 5 to 15 plants were found locally per square meter. Otherwise in low prairies where it is most abundant (occurring in 46 per cent) it ranked third place or, more usually, lower. In upland prairies it is nearly always found at the foot of moist slopes or near ravines except in those with greatest rainfall. It occurred in 25 per cent but ranked fifth in 18 per cent of these.

Oxalis stricta L., the upright yellow wood-sorrel, is a low herb of the grasslands. It was found in 25 per cent of the upland prairies, mostly in the moister areas but often widely even if not abundantly distributed. Here it ranked almost always in fourth or fifth place. In low prairies it was first or second in 4 per cent of the areas and in 20 per cent as a society of the third class. It was found in about half of the lowlands. Oxalis is also often abundant under slough grass and in other wet places. Very often it forms a definite and rather continuous layer in such habitats, as well as in the moist soil under big bluestem.

The plants vary from 4 to 14 inches in height depending upon the supply of water and the degree of shading. The stem is characteristically branched at the base and the branches are spreading. The leaflets of the trifoliolate leaves close when touched. The pretty lemon-yellow flowers are conspicuous

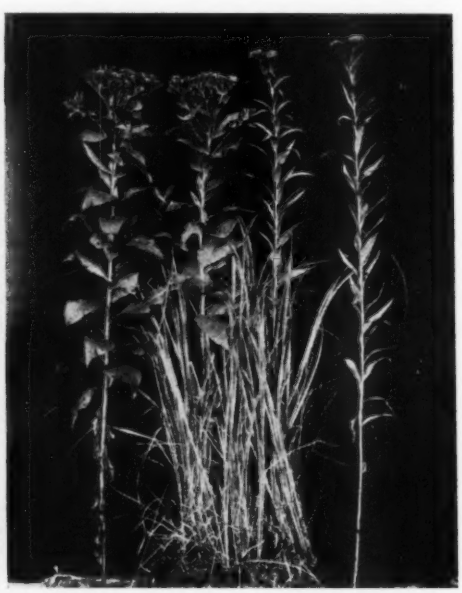

Fig. 93. *Lythrum alatum* 2.5 feet tall with grasses removed, June 24.
Fig. 94. *Vernonia fasciculata* (right) and *V. baldwini* shown in relation to the big bluestem on August 8. Note the defoliated lower portions of the stems.

among the grasses especially during spring and until midsummer although some plants may be found in bloom until late fall.

Oxalis violacea L., the violet wood-sorrel, is less widely distributed than *O. stricta* but often far more abundant. Like the yellow wood-sorrel it thrives best in low, moist soil. It was found in only 9 per cent of uplands and 14 per cent of lowlands where it usually occurred as a society of the second class or of lower rank. This stemless perennial propagates not only by seeds but also by small, brownish, scaly bulbs that occur in abundance. The leaves are usually larger—2.5 to 3 cm. wide—and darker green than those of the preceding species. The flowers are also larger and rose-purple in color, being conspicuous during May and June. This species where found usually occurs locally in considerable abundance and may form a dense society over an extensive area. In ravines and low, level ground as well as on moist, level uplands it is especially noticeable, often spreading beyond the limits of the big bluestem into wetter grassland types.

Persicaria muhlenbergii (S. Wats.) Small (*P. coccinea* (Muhl.) Greene) is a tall, gregarious perennial of swamps and moist soil. It was found throughout the entire area and in half of the low prairies where it usually ranked as a society of the third or fourth class, but in 8 per cent of the prairies it was in first or second place. This swamp Persicaria is perennial by long, thick, rather woody rhizomes. Consequently the plants, which are usually 2 to 4 feet tall, frequently form dense stands, but scattered groups and even isolated individuals are not unusual. The stems are usually quite erect and though sometimes branched near the base they are usually simple. The rather large leaves, which are 2.5 to 8 inches long, are sometimes covered with long hairs which give them a silvery sheen. They are rather widely spaced, but where the plants are sufficiently abundant they cast a dense shade. Beneath a dense group only a sprinkling of the most tolerant grasses and sedges are to be found. The leaves have fallen by midsummer from the first 15 to 20 inches of stem, exposing the enlarged nodes.

This species occurs regularly in stands of Elymus and Panicum or in areas of Spartina and is frequently relict in those occupied by *Andropogon furcatus*. It is also a regular constituent of socies of earlier stages of development, such as Eleocharis and *Carex vulpinoidea*. Where a dense sod of grasses occurs it is greatly handicapped and usually few in numbers.

This Persicaria renews growth very early in spring and for a long time outstrips the grasses in rate of growth. The dark rose-colored, erect racemes, of which there are only 1 or 2 per plant, develop in July or later. They are 1 to 3 inches long and where abundant add a pleasing tone to the vegetation.

Phlox pilosa L. is a perennial of unusually interesting distribution. It occurs abundantly on both lowlands and high prairies, even ranging over the hilltops in Iowa and Missouri. Westward it is nearly confined to low

ground and becomes less abundant with decreasing rainfall. Except where it has migrated into the drier climate along the flood plains of rivers, it practically disappears and is not found on the rolling uplands in the drier prairies in the western part of the area.

This plant, which is rather inconspicuous before blossoming, has slender, nearly erect stems 1 to 2.5 feet high (Fig. 97). When young the tops are reflexed in a characteristic manner. They appear early, occurring singly or in small clumps and for a long time stand well above the grasses. There are no runners or prostrate leafy shoots. The long narrow leaves are too few to shade the grasses to any considerable degree although there are sometimes 5 to 15 stems to the square foot. The large clusters of beautiful pink-purple or rose-red flowers are a conspicuous feature of the landscape during May and June. Even a single plant is noticeable at a considerable distance. The foliage remains green until fall and the dried inflorescence intact.

This phlox occurred in about 30 per cent of the uplands, usually ranking in first or second place, and in 44 per cent of the low areas. Here it held first rank in 27 per cent and second in 13.

Pycnanthemum flexuosum (Walt.) B. S. P. (including *P. virginianum* (L.) Durand & Jackson), the mountain mint, occurred as a society of the first class in 16 per cent of the low prairies (eastward) and in lesser abundance in 4 per cent of the lowlands. In a few cases it was found in the best watered uplands. This mint has stiff, slender stems that arise from a network of rhizomes. Hence, the plants occur ordinarily in fairly dense clumps or societies. Where conditions for growth are most favorable, 10 or more stems are found per square decimeter but usually they are more widely spaced among the grasses (Fig. 95). The linear to lanceolate, opposite leaves are borne on stems that are simple except for short leafy branches arising from the axils. The plants vary from 18 to 32 inches in height and are usually no taller than the surrounding grasses. The leaves are so narrow that those of an individual stem cast little shade. Moreover, the basal ones die by midsummer and the stems are mostly defoliated to a height of 3 to 8 inches. But where the stems are densely grouped the grasses are sparse over considerable areas. The inflorescence consists of dense clusters of tiny white flowers grouped in terminal, corymbed, dense glomerules. When in blossom, during July and later, the societies are very conspicuous. This mint has a pleasing fragrance.

The poison ivy, *Rhus toxicodendron* L. (*Toxicodendron rydbergii* (Small) Greene), is a frequent constituent of the prairie flora. It was found in 31 per cent of the high prairies and in a slightly larger proportion of the low ones. In the latter it ranked as a society of the first class in 3 per cent of the prairies, but otherwise it usually held third or fourth place. It is found rather regularly along ravines and fence rows from which vantage ground it spreads by rhizomes well into the grassland. On uplands it may

FIG. 95. Portion of a society of *Pycnanthemum flexuosum* on low ground on July 27. The grasses have been removed.

FIG. 96. Detail of poison ivy, *Rhus rydbergii*, in prairie on June 4. "Leaflets three, let it be."

also occur about rock ledges where there is seepage but sometimes it is found in deep soil of low prairies far from ravines or thickets.

During the early part of the year this familiar species occupies a place well above the grasses and receives full sunlight (Fig. 96). But later it is more or less overtopped by the grasses, since, because of annual mowing, it seldom reaches a height greater than 8 to 20 inches. The big bluestem, of course, is much taller. The broad, flat, smooth, thick leaflets shade the grasses considerably as the poison ivy spreads over them. Hence, one can readily detect the presence of a society of poison ivy upon approaching it. The creamy white fruits are conspicuous along unmowed ravines in fall and winter.

Rudbeckia hirta L. is a beautiful composite whose large orange-yellow blossoms are conspicuous from late June until well into August. It is gregarious in habit and usually forms dense and often also extensive societies. These, except along the Platte River, occur for the most part in the wetter portion of the general area. The species ranges from the margins of sloughs throughout the low prairies. Eastward, especially, it is found in the little bluestem prairies even on high uplands. Its preference for moist soil is shown by its occurrence in only 18 per cent of the high prairies (where it ranked first in only 8 per cent of them) but in 32 per cent of the lowlands. But here it was usually a society of the third or fourth class. The common name "black-eyed Susan" undoubtedly originated from the very dark color of the disk flowers. The flower heads are 7 to 9 cm. broad and sometimes occur at the rate of 100 to the square meter. They just overtop the big bluestem at heights of 24 to 30 inches (Fig. 98).

Senecio aureus L., the golden ragwort, is a perennial that varies in height from 0.5 to 2.5 feet. It occurs commonly on low ground in the big bluestem and wetter grassland types, often as an understory in slough grass. Where the precipitation is greater, however, it extends far up over the hills, decreasing somewhat in stature and even where best developed it is only about half as abundant as on lowlands. The plants are typically aggregated into dense, more or less circular areas a few feet to a few yards in diameter. The long, much dissected cauline leaves are not abundant; in fact, the upper half of the stem is almost naked. But the characteristic long petioled, ovate-cordate basal leaves often constitute 50 to 90 per cent of the ground cover in spring. Where this species occurs, it is nearly always found in abundance. Frequently it adds a yellow tone to the landscape over large areas and is discernible at a considerable distance.

Blossoming occurs late in April and continues throughout May. Early in June the clusters of large, orange-yellow flowers give way to the hoary heads of fruits which are widely distributed by the wind.

Silphium integrifolium Michx., the entire-leaved rosinweed, is a tall, coarse perennial that often forms large clumps especially in low ground. It

FIG. 97. *Phlox pilosa* showing its height (about 2.5 feet) in relation to that of the big bluestem early in June.

FIG. 98. *Rudbeckia hirta* in big bluestem sod, Columbus, Nebr., July 8.

is found only sparingly in uplands, except in the prairies with the greatest rainfall, and is almost confined to ravines and lowlands in the western part of the area. The clumps may consist of a few stems or there may be 15 to 24 or more (Fig. 99). The somewhat circular basal area thus occupied varies from a few inches to 4 feet in diameter and the stems, which are 3 to 7 feet tall, have a top spread of 2.5 to about 5 feet. Where the clumps are small and open they have little harmful effect upon the grasses; but under larger clumps the usual prairie grasses have disappeared and bluegrass alone, often in a thin stand, shares the area. Often even this tolerant species has been starved and bare areas of 3 to 4 square feet occur. Hence, where the plant is at all abundant the yield of prairie hay is reduced. A few low prairies were found where 20 plants occurred in a single square rod.

The rosinweed is among the first to appear in spring. Drawing upon the large stores of food in the thick crowns and extensive underground parts, it soon develops enough leaves to cover more or less completely the soil within the basal area of the clump. Soon the stems begin to elongate and in July they have reached almost full stature when the large flower heads begin to appear. The leafy stems are usually defoliated at the base; they are branched only near the top. Flower heads are numerous, 5 to 20 per plant; some arise from the axils of the leaves two-thirds of the way up the stem.

This Silphium occurred in 36 per cent of upland prairies but ranked as a first or second class society in only 8 per cent. On lowlands it was found in two-thirds of the areas and its ranking was rather evenly distributed in the five classes; in 15 per cent it ranked first.

Teucrium canadense L., the American Germander, is an important herb of wide distribution. It was found in 83 per cent of the low prairies, ranking first in 14 per cent and second and third in 9 and 29 per cent, respectively. This perennial, odorless mint springs from coarse, much branched, underground stems that are well supplied with whorls of fibrous roots (Fig. 100). Although the stout erect stems may occur singly or in small groups, they are often more or less densely aggregated into large ones. Societies with 50 or more stems to the square meter are sometimes found over rather large areas. The lower stems usually defoliate to a height of about a foot by midsummer but even then the dense upper foliage may have a detrimental effect upon the grasses. The rigid, square stems, with their rather large leaves regularly spaced in 4 rows, reach a height of 1 to about 3.5 feet, including the terminal, dense, wand-like racemes which, when mature, are 6 to 12 inches long. The rather small, light purple, or pink flowers would not be at all conspicuous except that many of them are closely grouped. This lowland species starts growth early in spring and develops rapidly, reaching its full stature in June when the spikes are formed. It blossoms throughout the summer.

Thalictrum dasycarpum Fisch. & Avé-Lall, the tall meadow rue, occurred in nearly half of the lowlands but held the rank of a first or second class

FIG. 99. A rosin weed, *Silphium integrifolium,* 5 feet tall with defoliated stems in the big bluestem. Photo. August 15.

FIG. 100. Stems of *Teucrium canadense* showing defoliated bases to height of grass (about 12 inches) and underground stems. Photo. June 24.

FIG. 101. *Silphium perfoliatum* in full bloom at a height of about 7 feet. Cherokee, Ia., August 8.

society in only 9 per cent. This stout, erect, often slightly purplish plant renews growth very early, and in the foresummer attains a height of 3 to 7 feet. Sometimes small plants 2.5 to 3 feet tall occur singly but they usually form a dense growth whether the community is large or small. The large, 3 or 4 ternately compound leaves may constitute 60 to 80 per cent of the foliage cover over areas of several square meters. Where competition is severe, the plants are less vigorous, but they are greatly aided in the struggle for light by their early renewal of growth. By August the stems are defoliated to a height of 8 to 24 inches. Blossoming of the tiny, dioecious flowers on the leafy compound panicles occurs from June until midsummer. The whitish flower clusters are often a foot or more in length and are very conspicuous. This plant remains green until frost.

Vernonia fasciculata Michx. is an indicator of moist to wet soil. It occurs throughout the entire region and was found in two-thirds of the low prairies. In three per cent only did it rank as a society of the first class, but in 8 per cent in the second rank, and in 40 in third or fourth place. This western ironweed is a coarse, erect perennial that reaches a height of 2 to 6 feet. The stems, which are mostly unbranched, occur singly or in small groups. The stiff stems are rather thickly clothed with numerous, firm, lanceolate leaves which are 3 to 6 inches long (Fig. 94). Their total spread seldom exceeds 5 inches, however, and even where 18 or more stems are found on a single root (which is unusual in undisturbed prairie) they are so

distantly spaced that they have little effect upon the grasses. Intolerance to shade is shown by the early dropping of the lower leaves to a height of 8 to 12 inches. In fact the lowest leaves are linear and scale-like in appearance. The plant is provided with thick, woody rhizomes and very numerous, rather fleshy roots. Flowering occurs during the autumnal aspect and the compact inflorescence of purple flower heads is a marked feature of the autumnal landscape, since they are plainly seen above the level of the grasses. This species increases greatly under grazing, becoming a noxious weed in lowland pastures.

Vernonia baldwini Torr., an ironweed, is a species of no great importance but of wide distribution and of peculiar interest. It is a tall, coarse, very leafy perennial that resumes growth late in April and is often 2 feet high by the first of June. When fully developed it has added another foot or two to its stature but at the same time has lost most of its lower leaves. The great clusters of purple flowers appear after midsummer and are conspicuous in the autumnal aspect. It nearly always occurs as isolated stems or in groups of 2 or 3 (Fig. 94). Confined to low land and ravines in the drier parts of the area, in the southeast it occurs on hilltops as well, but never in large clumps or in abundance. Even in lowlands it ranked highest, 18 and 20 per cent, as a species of third and fourth class. But when disturbance such as grazing occurs and reduces the competition of the grasses this Vernonia is benefited. The leaves are bitter and not eaten by stock. It rapidly increases its area and develops large bush-like clumps 1 to 3 feet in diameter. Thus while held in check in nature, interference with the biological balance converts it into a serious weed. It is thus a reliable indicator of disturbance.

The American vetch, *Vicia americana* Muhl., is a small, showy, trailing herbaceous vine which sometimes forms dense but limited societies in moist soil. Its importance as a constituent of the vegetation is small, since it was found in relatively few areas. It never ranked higher than a third class society and usually it was in fourth or fifth place. The large, bluish purple flowers of this pea vine are most conspicuous and abundant in May. As the grasses increase in stature this little plant is all but obscured.

The meadow or hooded blue violet (*Viola papilionacea* Pursh) is a species common to abundant in low prairie. Although found in only 11 per cent of the uplands, it occurred in 60 per cent of the low prairies, holding the rank of a first, second, and third class society in 14, 6, and 11 per cent, respectively. This stemless plant arises early in spring from a stout, branched rootstock. The long peduncled flowers are abundant in May. The bunches vary greatly in size; small plants have a dozen leaves or less and only 3 or 4 flowers; very large clusters sometimes have a basal area of 6 to 8 square inches and a spread of tops of a foot or more. Such clumps have hundreds of the large, broad leaves and scores of flowers. Plants of medium size with 10 to 18

of the deep violet flowers frequently occur at the rate of 5 to 10 per square meter where thickest on low ground. Where they occur as an understory in the shade of big bluestem or slough grass they attain a height of 8 to 10 inches, but usually they reach scarcely half this stature. The ovoid, cleistogamous flowers occur on horizontal peduncles which are usually underground. These lengthen and become erect with the ripening of the dark purple or green capsules.

Zizia aurea (L.) Koch is an important species of low prairie, being found in half of those studied. Moreover, it ranked as a society of the first class in 19 per cent of them. It occurred on uplands only in the wettest portions of the general area and then infrequently. The golden meadow-parsnip is an erect, glabrous, branched perennial that reaches a height of 1 to 3 feet. It arises in early spring from thick, short, underground stems well provided with thick, somewhat fleshy, fibrous roots. The plants may be distantly separated, or so densely grouped as to form a more or less continuous understory on lowlands in late summer. Except for the leafy flower stalks, an average height of the foliage of 1 to 2 feet is attained. Although there are often only 1 to 8 stems per plant, the many basal and lower long petioled leaves, which are bi- or triternately compound, give it a bushy appearance (Fig. 22). The cauline leaves are relatively few and smaller. The tops spread widely, often 3 feet from a basal area only 6 to 8 inches in diameter. About the base the soil may be much shaded and the ground nearly bare; in other cases a half-stand of big bluestem may overtop the foliage level. In places, Zizia has more or less complete possession of areas 15 or more feet in diameter, but in most instances there is at least a light sprinkling of the tall grasses.

The flower buds appear early and the yellow-flowered umbels are conspicuous. Blossoming occurs during May and June and the fruits are noticeable until fall.

The leaves are very tolerant of shade; many of the basal ones continue growth and new ones unfold after flowering and fruiting have been completed. They often double the amount of foliage and greatly increase the shade compared to that present at the time of anthesis. The foliage cover of grasses above this leafy layer is reduced one-third or more.

Of the remaining species, many are very large, coarse herbs. The cup plant, *Silphium perfoliatum* L., usually reaches a height of 5 to over 8 feet, the several stems and coarse leaves occupying much space (Fig. 101). *Helianthus maximiliani* Schrad. is usually somewhat taller, abundantly supplied with rigid leaves, and, like the preceding, indicates rich moist soil (Fig. 108). The sneezeweed, *Helenium montanum* Nutt., is of smaller stature, but frequently attains a height of 4 to 6 feet. All considerably shade the grasses. *Artemisia ludoviciana* Nutt. usually forms rather compact societies; *Monarda fistulosa* L. is a many-stemmed, tall, rather bushy mint. The Canada golden-

rod (*Solidago canadensis* L.) attains a height of 3 to over 4 feet and thus makes a place for itself among the grasses. The four o'clock, *Allionia nyctaginea* Michx., although a large coarse herb, has a branched, widely spreading, but fairly open top 3 or more feet high. All of these species are long-lived perennials and all but Allionia, which blossoms early, contribute to the variety and abundance of flowers of the autumnal aspect.

Amphicarpa pitcheri T. & G. and *Lathyrus palustris* L. are trailing leguminous vines, the former especially often spreading widely over the grasses. *Allium canadense* L., *Physalis virginiana* Mill., and the annual species, *Chamaecrista fasciculata* (Michx.) Greene, are plants of only moderate size growing at or below the midsummer level of the grasses. The stately, single stemmed *Lilium canadense* L. usually reaches a height of over 3 feet. The leafy *Potentilla monspeliensis* L. and coarse-leaved *Cirsium undulatum* (Nutt.) Spreng. both may attain a similar height, although the rosettes of the latter probably have the most profound effect upon the grasses. The leaves of the rosettes of Gaura and of *Oenothera biennis* L. are finally carried up into the light by the elongating stems, usually to a height of 2 or more feet. The habit of *Lobelia spicata* Lam. is variable depending in part upon the surrounding vegetation and the resulting struggle for light. Sometimes the bluish white flowers are held 2 to 3 feet above the surface of the soil.

Distribution

In addition to the 142 species in Tables 15 and 16, more than 200 others were listed for the several types of grassland. The list would have been much longer had developmental stages been included. But among these species none was found to occur in even 10 and often less than 5 per cent of the 135 prairies studied. Some of these species were met only in a certain section of the area or at least occurred but rarely elsewhere. For example, in the northern prairies the following were found: *Amorpha nana* Nutt., *Pulsatilla ludoviciana* (Nutt.) Heller, and *Ranunculus ovalis* Raf. Eastward *Melanthium virginicum* L., *Viola pedata* L., *Eryngium yuccifolium* Michx., and *Spiranthes gracilis* (Bigel.) Beck occurred. Southward such species as *Houstonia angustifolia* Michx., *Baptisia australis* (L.) R. Br., *Commelina crispa* Wooton, and *Viorna fremontii* (S. Wats.) Heller were found. From the west and especially the southwest there are numerous floral elements, many of which are not represented, or at least but sparsely farther eastward. Representative of these are the following: *Chrysopsis villosa* (Pursh) Nutt., *Yucca glauca* Nutt., *Opuntia fragilis* (Nutt.) Haw., *Sideranthus spinulosus* (Pursh) Sweet, *Hosackia americana* (Nutt.) Piper, *Malvastrum coccineum* (Nutt.) A. Gray, and *Talinum parviflorum* Nutt.

Certain other species may be found bordering woodlands, groves, or other sheltered localities. Among these may be mentioned *Clematis virginiana* L., *Cornus stolonifera* Michx., *Vitis vulpina* L., and *Zanthoxylum americanum*

Mill. These species are representative of many others that were found in relatively few prairies. A few prevernal forms such as *Erythronium mesochoreum* Knerr and *Nothocalais cuspidata* (Pursh) Greene, may have been more abundant than 5 to 10 per cent, but certainly their early disappearance renders them of small significance as components of the plant cover.

An examination of Table 15 shows that of the ten most important upland forbs, two are legumes and eight are composites. In fact, among the 75 most important forbs of the upland prairies, species of composites and legumes are by far the most numerous. The Compositae rank highest, constituting one-third of the whole group. The Papilionaceae contribute 17 per cent. The Asclepiadaceae and Boraginaceae each constitute slightly more than 5 per cent. Six other families each contribute 2.7 per cent, viz.: Ranunculaceae, Scrophulariaceae, Rosaceae, Labiatae, Iridaceae, and Polygalaceae. No other family, in this list of most important forbs is represented by more than a single species. Thus seventeen families contribute to supply the remainder, about 23 per cent.

A study of Table 16 shows that five of the ten most important forbs of lowlands are composites, but that the remaining five are each representatives of different families. Of the 67 leading species of forbs of low prairies, 34 per cent are Compositae; 9 per cent Papilionaceae; 6 per cent Labiatae; and 4.5 per cent Asclepiadaceae. Eight families contribute 3 per cent each, viz.: Ranunculaceae, Rosaceae, Onagraceae, Solanaceae, Liliaceae, Geraniaceae, Umbelliferae, and Equisetaceae. Fifteen other families contribute the remaining 22 per cent.

Considering the prairies of both uplands and lowlands as a unit, the Compositae furnish 34 per cent of the leading species of forbs. The Papilionaceae contribute 13 per cent. The Asclepiadaceae and Labiatae rank next, furnishing about 5 and 4 per cent of the species, respectively. The Boraginaceae contribute slightly more than 3 per cent; the Rosaceae, Ranunculaceae, and Onagraceae each only slightly less. The following five families each constitute about 2 per cent, viz.: Iridaceae, Scrophulariaceae, Solanaceae, Liliaceae, and Umbelliferae. Six other families contribute about 1.5 per cent each: Campanulaceae, Violaceae, Nyctaginaceae, Equisetaceae, Geraniaceae, and Polygalaceae. No other family furnishes even 1 per cent of the species of much ecological importance; the remaining 13 or 14 per cent being distributed among nineteen different families.

HEIGHT CLASSES

The forbs of both low and high prairie, listed in Tables 15 and 16, may be grouped approximately into three classes: those that have little or no foliage exceeding a height of 1 foot on uplands and 1.5 feet on lowlands; those whose leafy stems function mostly at a height of about 2 feet; and a third class

where many of the leaves are carried far above 1.5 to 2 feet which is approximately the midsummer level of the grasses.

On the lowlands, the first group is the smallest including such plants as *Fragaria virginiana* and *Viola papilionacea*, and a total of 19 per cent of the species. The second one with *Steironema ciliatum*, *Zizia aurea*, and plants of similar stature is intermediate with 31 per cent. The largest group, with 50 per cent, includes coarse herbs such as species of Silphium, Helianthus, and Vernonia.

On the uplands, the first class is represented by approximately 31 per cent of the species. This group of low growing plants is represented by such species as *Antennaria campestris*, *Viola pedatifida*, *Astragalus crassicarpus*, etc. The second group is by far the largest, including about 39 per cent of the species. Plants of intermediate height are well represented by *Aster multiflorus*, *Erigeron ramosus*, and *Rosa arkansana*. The third group, which includes tall plants, is represented by only 30 per cent of the species in the lists. Here are to be found, for example, *Psoralea floribunda*, *Ceanothus pubescens*, and *Baptisia leucantha*.

This classification, however, is not absolute since many of the lowland forms also occur on upland prairie. But perhaps still more of the taller upland species are also found in the lowlands. The greater stature of many of the lowland forms probably results in part from a greater abundance of available water and generally less xeric environment on the one hand, and from the long struggle for light in competition with the tall grasses on the other. Numerous light-demanding, upland species, were they transferred to low ground, would be quite submerged by midsummer under the denser and taller cover of grasses.

SEASONAL ASPECTS

The prairie presents four distinct seasonal aspects, besides the more somber one of winter, into which the preceding species are more or less naturally grouped. Their initiation in spring and their duration vary considerably with latitude and to a smaller degree with slope and exposure. The approximate dates given for each aspect apply particularly to the central portion of the area. They begin about 10 to 14 days earlier on the southern border and 7 to 13 days later on the northern edge of the region.

The prevernal aspect begins with the growing season, usually late in March, and continues to about the last week of April. May is definitely characterized by the vernal aspect, and June and much of July by the estival. From late July until frost the autumnal aspect holds sway. The orderly succession of changes in the conspicuous features of the landscape proceeds with marked regularity. If temperature and moisture conditions are less favorable, the time relations, which perhaps depend largely upon natural periodicity in relation to the length of day, are but little changed. The pre-

vernal aspect, for example, may be less pronounced because of cold or drought hindering the usual development of the societies, but nevertheless it does not merge with the vernal. Nor does the estival aspect encroach upon the autumnal even if the midsummer has been so dry as to prevent the usual wealth of flowers by which it is characterized. It is merely less characteristic because less developed. Aside from the factors of increasing or decreasing intensity of insolation and differences in length of day, the seasonal aspects can not be separated upon the basis of change in habitat factors, such as water content of soil (cf. Thornber, 1901; Harvey, 1908; Weaver and Himmel, 1931).

PREVERNAL ASPECT

The earliest prevernal bloomers appear in the warmer situations late in March or early in April. The most important are *Carex pennsylvanica* and *Antennaria campestris*. Both are low perennials and hence conspicuous only because of their gregarious habit and the fact that few other plants appear at this season upon the brown background of dry grasses and herbs. The sedge often forms patches or mats several meters in extent which are rendered conspicuous by the yellow and purple of the numerous small spikes. The prairie everlasting is a stoloniferous mat former and this with its white-woolly appearance makes it one of the most conspicuous elements of the prevernal flora (Fig. 111).

Among other prevernal bloomers is the modest little windflower, *Anemone caroliniana*, arising from a tuber (Fig. 102). The showy dog's tooth violet, *Erythronium mesochoreum*, develops very early in moist soil from a deep, solid, scaly bulb. It usually forms extensive local societies. In the northern portion of the region especially, the pasque flower, *Pulsatilla ludoviciana*,

FIG. 102. Windflower, *Anemone caroliniana*, in high prairie on May 1.
FIG. 103. Detail of *Callirrhoe alcaeoides* showing fleshy root, variations in leaves, and flowers. Photo. June 12.

opens its pale lilac petals early in April on dry uplands. It is almost equally conspicuous later, however, when in its fruiting stage it flings to the breeze its silvery, plumed achenes. The pale cones of *Equisetum arvense* add local color to the landscape as do also the much branched stems which develop somewhat later. *Antennaria plantaginifolia* is fairly common on the moister soils and the dense patches are often very conspicuous. *Cogswellia foeniculacea* and *C. daucifolia* frequent dry ridges; *Ranunculus ovalis* is an early bloomer northward; *Draba caroliniana* and *Androsace occidentalis* are conspicuous only when very abundant.

This aspect marks the anthesis of only a small number of species. *Stipa spartea, Koeleria cristata,* and *Elymus canadensis* are the only dominant grasses that have made considerable growth, but this is exceeded by the rapid development of *Poa pratensis.*

VERNAL ASPECT

Late April introduces the vernal aspect. The drab tone of winter is, in general, replaced by the greenish tinge of the new growth of grasses. The dominant bluestems renew growth about the middle of April, but on lowlands and north slopes the colors of the dried vegetation of the preceding fall are often not entirely obscured until the first week in May. Needle grass and June grass, of earlier awakening, add verdure to the landscape as may also Elymus on low ground. Bluegrass is now so far advanced that the production of flower stalks is beginning.

This period initiates rapid vegetative growth of plants of summer and autumn as well as those of spring. In the ravines and moist soil tall-growing forbs such as *Helianthus grosseserratus, Solidago altissima, Silphium integrifolium,* and other late bloomers far outstrip the grasses in rate of growth (Fig. 104). Others, mostly of early blooming habit, such as *Oxalis violacea, Fragaria virginiana,* and *Viola papilionacea* rapidly develop both foliage and flowers before the light is too much obscured by the growth of the grasses. The new shoots of blazing stars, goldenrods, sunflowers, and especially of species even more conspicuous because of their lighter color, such as sage and Psoralea, add tone to the landscape. Winter has gone, spring has come, and the prairies pulse with life. From the background of green show forth the gems of nature, manifold in variety, radiant in beauty, endless in recurrence—the societies of the vernal aspect.

The early vernal flora is marked by numerous species. *Hypoxis hirsuta* adorns many moist prairies. *Fragaria virginiana* is found abundantly, especially on low, moist ground. *Sisyrinchium angustifolium* and *S. campestre* are widely distributed and usually very abundant. *Viola pedatifida,* characteristic of the dry prairies, and *V. papilionacea* and *V. palmata* of the more moist ones, may occur as scattered individuals or more or less closely grouped.

FIG. 104. *Solidago altissima* and *Helianthus grosseserratus* in the margin of a ravine, showing height (about 32 in.) on June 15. On May 1 they were 10 inches high and they have always overtopped the grasses.

FIG. 105. A single plant of *Meriolix serrulata* in full bloom on June 4.

Sometimes 10 or more bunches are found per square meter. *Viola pedata*, found only rarely, is by far the most splendid of all the violets. Where 20 to 30 clumps per square meter occur, each with 30 to 50 large, pale blue flowers, they give a beautiful tone to the landscape.

The large plants of *Astragalus crassicarpus* show conspicuously with their abundance of purple flowers. *Senecio plattensis*, where at all numerous, adds a tinge of yellow to the drier prairies but is often more abundant on the lowlands. It is less conspicuous than are the more dense societies of *Senecio aureus* which frequent moist soil. The puccoons—*Lithospermum linearifolium* with its lemon-yellow flowers, *L. gmelini* and *L. canescens*, both with their numerous blossoms of orange—like the senecios show conspicuously since their flowers also occur usually eight or more inches above the surface of the soil. Numerous local societies of *Comandra umbellata* abound. *Carex meadii* is found widely, and the taller *Carex festucacea* on lower slopes and moist ground. Numerous other carices of wet soil such as *C. vulpinoidea* and *C. hystricina* are also in blossom. Here too the spike rushes, *Eleocharis palustris* and others, are in flower.

The white flowers of *Allium nuttallii* show abundantly in extensive societies among the plants of lowlands; the yellow ones of the false dandelion, *Nothocalais cuspidata*, are found in open rank on higher ground. The large cream-colored racemes of *Baptisia leucophaea* are conspicuous even at a distance as are also the erect spikes of the yellow or reddish flowers of *Pedicularis canadensis*. Great patches of *Vicia americana* occur locally, their clusters of purplish flowers being very attractive. Most other early vernal bloomers are fewer or far less conspicuous.

FIG. 106. Society of *Oxalis violacea* of the vernal aspect, under big bluestem.

Among the later vernal bloomers, *Anemone canadensis*, because of its habit of forming dense societies, is one of the most conspicuous of low moist soil. Beginning to blossom about the middle of May, the large white flowers for several weeks add variety to the landscape. The yellow of the golden parsnip, *Zizia aurea*, is a characteristic feature of many low prairies, moist ravines, and well watered uplands. The umbelliferous inflorescence is held 2 to 3 feet high and is very striking. The large cymes of the bright pink or purple of *Phlox pilosa* appear in the middle of May. They stand high above the grasses on the moist hillsides and indicate by their greater abundance the more favorable moisture relations along ravines or on flood plains. They continue to bloom far into the estival aspect.

Many hill crests and rugged slopes during May are adorned with the white masses of flowers of *Ceanothus pubescens*. The conspicuous trifoliolate leaves and rose-purple flowers of *Oxalis violacea* are found in the understory of many moist prairies and slough-grass swamps (Fig. 106). The yellow flowers of *O. stricta* occur abundantly in similar habitats and along ravines; the species occurs also in upland prairie. The tiny white flowers of *Galium tinctorium* would be scarcely noticeable except that the plants are densely aggregated, frequently forming a continuous layer under the tall grasses and sedges of ravines and wet soil. The abundant dark green stems of *Equisetum laevigatum*, each terminated by a brownish cone, often add to the aspect. *Tradescantia bracteata* and *T. virginiana*, the latter especially in sandy soil, add a definite purple to the landscape where they occur in numbers. The pink or white flowers of *Callirrhoe alcaeoides* and the purple of an occasional *Oxytropis lambertii* further enhance the beauty of the prairie in spring (Fig. 103).

ESTIVAL ASPECT

The estival aspect begins during the last week in May. By this time *Poa pratensis* has blossomed, the spikes of *Koeleria cristata* are beginning to open, and *Stipa spartea* is often in full bloom. Several minor grasses, notably interstitial species of Panicum, are beginning to expand their purplish, feathered stigmas to the breeze. The bluestems and other dominant grasses now cover the uplands with a deep foliage of green and on the lowlands a height of 12 to 18 inches has been attained.

Among the forbs there is a distinct transition from spring to summer. The showy flowers of *Baptisia leucophaea*, species of Sisyrinchium, *Senecio plattensis*, and many others are gone or at least they are being replaced by fruits. The landscape is rapidly becoming redecorated with extensive societies of Erigeron, various psoraleas, and the rose. Several vernal species continue to bloom; Ceanothus on the uplands, Phlox, Oxalis, and Tradescantia on both high and low ground; and on the lowlands there persist great areas of *Anemone canadensis*, *Zizia aurea*, *Galium tinctorium*, *Callirrhoe*

alcacoides, and the ripening *Senecio aureus*. But these are soon to wane and are rapidly being replaced by an increasing wave of estival bloomers.

Psoralea floribunda, where at all abundant, gives a distinctive tone to the landscape. The bushy tops stand well above the level of the grasses and the countless clusters of small blue flowers mingled with the light gray of the leaves contrast strikingly with the verdure of the grasses. Flowering continues 3 to 4 weeks. Lower hillsides and steep slopes along ravines are

FIG. 107. Prairie larkspur, *Delphinium virescens*, about 3 feet tall.
FIG. 108. *Helianthus maximiliana* of low prairie, standing high above the foliage level of big bluestem which is nearly 3 feet. Photo. Sept. 8.
FIG. 109. Two plants of *Allium mutabile* about 12 in. tall (center) and two of *Allium canadense*, characteristic of the estival aspect.

frequently covered with extensive societies of the silvery leaved *Psoralea argophylla*. Although the small blue flowers are neither abundant nor conspicuous, the societies are clearly differentiated and occur widely in the majority of the prairies. The less showy and far less abundant *Psoralea esculenta* blossoms somewhat earlier than either of the preceding, being in part prevernal.

Extensive areas of both uplands and lowlands are covered, especially during drier years, with the erigerons. The showy white flowers are often so thickly grouped that they are conspicuous from afar. *Erigeron annuus* and *E. philadelphicus* are the larger plants, but even the smallest of the three common species *(E. ramosus)* well overtops the grasses. Hence where even isolated plants occur the white bouquet of flowers is held well above the sea of green. *Achillea occidentalis* groups its tiny white flower heads in corymbs which, though the plants are seldom abundant, add tone to the landscape.

June is also the month for roses. On both the uplands and lowlands the white and pink tinted buds and blossoms of *Rosa arkansana* add beauty to the grassland. Even single large flowers are attractive but usually they occur in groups. Rosa continues to bloom well into July.

Standing far above the surrounding vegetation, the larkspurs, sentinels of the prairie, display their racemes of large white flowers (Fig. 107). Late in June, *Delphinium virescens* is replaced by the tall stalks and whitish flower clusters of *Mesadenia tuberosa*. By the middle of July the tiny yellow flowers that terminate the wand-like stems of *Hieracium longipilum* also appear. Their elevated position above the dominants is shared by *Baptisia leucantha*, a coarse herb usually with single stem, and tree-like spreading top. The central of the several large terminal racemes may attain a height of 5 feet. The great clusters of cream-colored flowers are prominent features in the landscape as are also the inflated pods which persist into late fall.

Species of smaller stature but often of greater local abundance include the white and pink flowered *Allium mutabile* and *A. canadense* (Fig. 109); the white flowered *Polygala alba* and *P. viridescens;* the several species of Physalis scattered singly here and there with their pale yellowish bell-like flowers and bladdery fruits; as well as the bluish flowered *Lobelia inflata* and *L. spicata*. The large yellow but ephemeral flowers of *Linum sulcatum* occur at about the level of the grasses or somewhat above them, but the shorter *Specularia perfoliata* is well hidden beneath.

The large, lilac, lavender blue or white flowers of the pentstemons add beauty to the prairie. *Pentstemon gracilis* has relatively small flowers but those of *P. cobaea* and *P. grandiflorus* are very conspicuous. But these plants occur infrequently although the last especially is abundant locally.

The large yellow flowers of *Meriolix serrulata* add to the aspect perhaps much more than any other of the evening primroses such as Gaura and Oenothera (Fig. 105). *Drymocallis agrimonioides* is too infrequent to be important as is also *Callirrhoe involucrata*. But where the latter does occur its abundant, large, deep red or purplish, mallow flowers are indeed impressive. By the middle of June, the bush-like *Asclepias tuberosa* puts forth its masses of orange-yellow to brick-red flowers which are conspicuous features in the landscape.

Another species giving character to the estival aspect is *Echinacea pallida*. The large, purple or rose colored ray flowers occur in considerable abundance at a height of 2 to 2.5 feet and are conspicuous 3 to 5 weeks. Southward the globose heads of pink flowers of the sensitive brier (*Morongia uncinata*) are very attractive.

On low ground several tall, coarse plants give variety to the seasonal aspect. The large white umbels of *Cicuta maculata* and the inflorescence of the dioecious *Thalictrum dasycarpum* may be seen from afar as may also the

large, purplish tinged, hemispherical umbels of *Asclepias sullivantii*. *Apocynum sibiricum*, 3 to 4 feet high, still overtops the grasses and conspicuously displays its pale cymose flowers. In moister areas are to be found the pretty, pale red flowers of *Asclepias incarnata* and the pinkish ones of *Persicaria muhlenbergii*.

The greenish flowers of *Toxicodendron rydbergii* make this obnoxious plant only slightly more noticeable, but the deep purple blossoms of *Lythrum alatum* immediately reveal the abundance of this species. A single flower of *Rudbeckia hirta*, with its black center and rays of gold, is conspicuous, and often large societies of this species adorn the prairie.

The small white flowers of the milk spurge, *Euphorbia corollata*, are held high above those of most other species as are also the white and pink heads of *Cirsium undulatum*. *Asclepias verticillata*, *Anemone cylindrica*, *Lygodesmia juncea*, *Astragalus canadensis*, and various species of Acerates occur in full bloom at intervals throughout the prairie. The stately plants and showy flowers of *Lilium canadense* and *L. philadelphicum* add further variety to nature's varicolored garden.

Myriads of flowers now contribute to the great wealth of midsummer beauty. Among the most distinctive and widely spread societies of upland is that of *Amorpha canescens*. Even before the abundant, dark purple flowers begin to appear late in June, the leaden-colored leaves give tone to the landscape. Blossoming is profuse and it continues several weeks. Many species of plants of most varied hues form the endlessly variable patterns. Bright yellow patches of *Coreopsis palmata* are found on many ridges and slopes. The yellow rays and cone-like centers of *Lepachys columnifera* and *L. pinnata* appear conspicuously in the landscape. *Ruellia ciliosa* is found among the grasses, but masses of the pea vine, *Amphicarpa pitcheri*, sometimes overrun the grasses. Great gray patches of *Artemisia gnaphalodes* adorn the lower slopes or moist lowlands, although this composite flowers later. Isolated but conspicuous plants of *Eryngium yuccifolium* locally dot the cover in some of the more mesic prairies.

The purple cones of *Petalostemon purpureus* vie in numbers and attractiveness with the white ones of *P. candidus*. *Parosela alopecuroides* occurs southward. The stately flower stalks of *Meibomia illinoensis* and of *M. canadensis* hold far aloft their terminal racemes of purple or purplish flowers.

In rich moist soil *Glycyrrhiza lepidota*, standing somewhat above the level of the grasses, puts forth clusters of pale yellowish flowers which are soon replaced by the equally conspicuous pods. The stately purple spikes of *Teucrium canadense* and the much more numerous but white racemes of *Leptandra virginica* proclaim at once the beauty of the prairie and a favorably moist habitat. The small white or purplish flowers of the water hoarhound, *Lycopus americanus*, though grouped in dense axillary clusters, are not so

conspicuous as the purple spotted ones of its fragrant-leaved, sister mint, *Pycnanthemum flexuosum*. These with *Mentha canadensis* and others adorn low wet ground. Here also *Steironema ciliatum* with its pretty lemon-yellow flowers is found, usually being more or less hidden by the rank growth of grasses and forbs. *Monarda fistulosa* is a conspicuous taller species of moist soil. Its blossoms are large, conspicuously grouped into heads, and of an attractive rose-red color.

Near the close of this aspect certain coarse composites come into bloom. The upland prairies as well as many on lower grounds take on further color with the blooming of *Silphium integrifolium* and of *Helianthus rigidus*, the latter being found almost everywhere. The orange-yellow flowers of *Heliopsis scabra* also appear and the very numerous yellow rays of the clustered heads of the cut-leaved rosin weed *(Silphium laciniatum)* are indeed a conspicuous feature of the prairie.

Many other flowers adorn the rolling hills and lowlands. The patterns are endlessly variable in detail. Each week new elements appear and old ones gradually decline as the season advances. At nearly all times the prairie-garden is beautiful. The advent of severe drought, however, at some period during the growing season, may seriously handicap the usual wealth of blossoms and indeed flowers may become rather rare.

The blooming of the sunflowers and the yellowing of the inflorescences of the goldenrods portend the coming of fall. Once more the scenes are shifted as the estival aspect in July gives way to the oncoming of the autumnal one

AUTUMNAL ASPECT

About the middle of July the prairie begins to change gradually in appearance. The graceful flower stalks and inflorescences of *Bouteloua curtipendula*, which have been developing slowly, now appear in abundance for the first time. The spikes of nodding wild rye are nearing the height of anthesis. Soon the panicles of *Panicum virgatum* begin slowly to unfold, and isolated stalks of the bluestems overtop here and there the vegetative growth which has now nearly completed its development. The deep cover of grasses, 14 to 18 inches on the uplands and 2 to 3 feet on moist ground, although still green and vigorous, has passed from a stage of active development to one of approaching fruition and maturity.

Most of the estival plants have finished blooming; others are distinctly on the wane; but many continue into the autumnal aspect at least for a time. For Rosa, Phlox, Psoralea, and Zizia one must await another year. The flowers of Amorpha, Coreopsis, and Steironema are likewise gone or nearly so. In upland areas and well drained soil Hieracium, Meriolix, Mesadenia, Drymocallis, Euphorbia, Petalostemon, and Meibomia are still to be found. Euphorbia, indeed, continues blossoming almost until frost and *Meibomia*

canadensis is at its height of blooming with its showy red or purple flowers, but *M. illinoensis* is distinctly past its prime. Rudbeckia is rapidly passing from the scene but *Cirsium undulatum*, *C. altissimum*, and *Eryngium yuccifolium* still stand bravely forth above the grasses.

On lower ground *Cicuta maculata*, *Apocynum sibiricum*, *Asclepias incarnata*, *Monarda fistulosa*, species of Pycnanthemum, *Teucrium canadense*, and *Leptandra virginica* are in their prime. Lycopus and Lythrum show forth from wet areas as do also the white or pinkish flowers of *Persicaria muhlenbergii*. *Chamaecrista fasciculata*, where it is abundant, is a sea of gold. The whitish flowers of *Asclepias verticillata* are still conspicuous and *Lepachys pinnata* adds beauty to the prairie wherever it is found.

The coarse composites that began blossoming near the close of the preceding aspect now develop in all their splendor. *Silphium integrifolium* dots the landscape where moisture is plentiful, its great stems, each often with a score of large yellow flowers, standing 3 to 5 feet in height. *S. laciniatum* is equally conspicuous and often far more abundant. In rich moist soil *S. perfoliatum*, with its great cupped leaves and bright yellow flowers, is found, but usually in less abundance. The gold of clumps of *Heliopsis scabra* recurs again and again. The blooming of the sunflowers, initiated by *Helianthus rigidus*, often continues until frost. Over the uplands, even in the driest soil, the small heads of *H. rigidus* are held singly or in two's or three's just above the grasses. On low ground its stature and number of flowers are doubled. *H. grosseserratus* is a conspicuous bloomer of late fall as are also *H. tuberosus*, *H. maximiliani*, and certain other species of ravines and moist soil (Fig. 108). In wet soil various species of Bidens with their yellow flowers are to be found.

The yellows and gold of the rosinweeds, rough oxeye, and sunflowers intermingle with the purple of the blazing stars. *Liatris squarrosa* and *L. pycnostachya* begin to blossom early in the aspect. Somewhat later they are reinforced by the blooming of *L. scariosa* and *L. punctata*. A single bushy plant of *L. scariosa* with its many stems and abundant heads of purple flowers is indeed a pleasing sight. But when, as in *L. pycnostachya*, the blossoms are crowded into gorgeous bouquets of thick spikes, 10 to over 12 inches long and held far aloft, they are indeed magnificent (Fig. 110). Nature presents her most gorgeous colors where societies of the blazing stars dot the landscape. Such beauty is scarcely surpassed. *L. punctata*, of smaller stature, adorns dry uplands. *L. scariosa* is slightly more mesic and has a somewhat greater height (2.5 to 5 feet); the purple heads are also larger and somewhat more attractive.

The blossoming of *Solidago glaberrima* portends the season of goldenrods. This species is the one most widely distributed among the prairie grasses. Its panicles of tiny golden flowers are held often just above the sea of green.

FIG. 110. Dense society of *Liatris pycnostachya* in a ravine near Cherokee, Ia., Photo. August 9.

FIG. 111. Society of fruiting *Antennaria campestris* on low ground near Tarkio, Mo., in May.

FIG. 112. Contact between deciduous forest and grassland about 2.5 miles west of the Missouri River, 20 miles north of Walthill, Nebr. Prairie in foreground and on both sides of ravine in distance where *Symphoricarpos vulgaris* is invading; maize in alluvial valley.

They frequently occur in great masses and add much beauty to the autumnal landscape. The yellowish buds of *S. rigida* open somewhat later and the great flat-topped inflorescences of gold are held aloft on the rigid stems. *Solidago rigidiuscula* adds its wealth of flowers to the uplands in late August or September. Even after blossoming is finished and the seeds are formed, the yellow involucres retain their color and the plants are conspicuous until late fall. In the lower ground, *S. altissima*, also a late bloomer, likewise tints the prairie with patches of gold. Other important autumnal bloomers are *S. canadensis*, *S. serotina*, *S. mollis*, and *S. nemoralis*. There are also numerous other goldenrods of minor importance.

Pleasing variety is added to the wealth of autumnal colors by the grayish white flowers of *Kuhnia glutinosa*. This species is more conspicuous, perhaps, after the flowers have ripened and the white pappus has developed on each of the abundant fruits. The sage, *Artemisia gnaphalodes*, is conspicuous throughout late summer and fall as are also the flowering and fruiting heads of *Lespedeza capitata*. The large yellow flowers of *Oenothera biennis* and the smaller ones of various species of Gaura add to the aspect as do also the purple flowers of *Vernonia baldwini* in ravines and low ground and *V. fasciculata* in wet soil. *Allium cernuum* sometimes locally brightens the grassland. *Helenium montanum* and *Euthamia graminifolia* are yellow composites contributing to this aspect. The tall *Salvia pitcheri* presents its wealth of large blue flowers in August and September. These stand in striking contrast to the deep red of the ripening fruits of the rose.

The asters blossom from August until late fall; several species reach their height of flowering late in September. Among the latter *Aster multiflorus* (including *A. batesii*) has a wealth of small white or purplish white blossoms which when well developed quite obscure the foliage. In dry uplands the masses of flowers scarcely exceed the height of the grasses. In ravines and on low ground, *A. salicifolius* affords a show of large white flowers. Those of *A. paniculatus* and several minor species are of similar color and abundance. The blue or purple flowers of *A. laevis*, *A. azureus*, *A. novae-angliae*, *A. sericeus*, *A. oblongifolius*, and others are interspersed here and there in the varicolored landscape during the latter half of the aspect. In late autumn, the deep blue flowers of *Gentiana puberula* may be found here and there hidden among the grasses.

During September and later fall, the great fields of fruiting grasses are beautiful to behold. On low ground scores of the forked inflorescences of big bluestem may occur on each square meter. The golden panicles of Indian grass glisten in the sun. The spikes of Spartina offer a pleasing pattern of a different variety and vie in splendor with the broad, delicate panicles of *Panicum virgatum*. The dried heads of nodding wild rye stand thickly in ravines while on uplands the abundant flower stalks and whitish fruits of

little bluestem add pleasing variety. Here also the open panicles of *Sporobolus heterolepis* are held aloft above the level of the foliage. The reddish panicles of the interstitial *Eragrostis pectinacea* also add a touch of beauty to the pleasing view.

About the first week in September, or earlier if the season is dry, Andropogon, *Panicum virgatum*, and Sorghastrum begin to lose their green color and slowly take on the red and bronze and golden tints of autumn. With the progress of the season, these gradually deepen until the landscape presents a color scheme rivaled in beauty and delicacy of painting only by the autumnal coloration of the great deciduous forest. Late October or November witnesses the waning and finally the death of the aerial parts of the forbs and grasses. But even the winter aspect does not lack charm and is often one of splendor.

HIEMAL ASPECT

The culmination of fruition and maturity of the autumnal blooming forbs and late maturing grasses occur in September and October. After this time there is a gradual deterioration of the vegetation, which is hastened by repeated frosts. The forbs have completed blooming, most of the inflorescences have fallen although the dried remnants of some, like the black heads of Echinacea, the brown ones of Lespedeza, the drying fruits of Rosa and Glycyrrhiza, the variously grouped heads of the goldenrods, and also those of Silphium and Helianthus, are still conspicuous. The dry or drying leaves may fall to the ground or cling as withered things to the bare stems. The leaves of the grasses dry in place on the erect stems without much change in outward appearance except that the wonderful shades of bronzes, reds, and gold gradually fade with the passing of the weeks to the various tints of gray or somber reddish browns.

The numerous, whitish, hairy spikelets on the racemes of *Andropogon scoparius*, so conspicuous in fall, are now nearly all carried away by the wind. The naked zigzag rachis of *Bouteloua curtipendula*, or perhaps with a few spikelets still attached, together with the dried flower stalks of *Koeleria cristata* and the now seedless panicles of *Sporobolus heterolepis*, are still to be found on uplands. On lower slopes and low ground are seen the dried panicles of *Sorghastrum nutans* with a few fruits that have withstood the whipping of the early winter winds. On low prairie the wide-spread panicles of *Panicum virgatum*, the spikes or "heads" of *Elymus canadensis*, and the finger-like racemes of *Andropogon furcatus* adorn the winter landscape. In wetter areas the great panicle-crowned stems of *Spartina michauxiana* stand yet in place, dry and bleached, in the winter's cold.

Although the grasses as well as certain forbs may remain intact for a long time (the dead stems often intermixed with the green ones of a second summer), yet as a result of natural deterioration, augmented by the work of

the wind and assisted by the weight of ice and snow, the once great cover of standing vegetation gradually returns to the surface of mother earth. Here it forms a protecting blanket to the living parts within and beneath the surface of the soil. Unless removed by fire, it decays but slowly throughout the coming seasons. Even in winter the prairies are attractive. One can readily identify all the genera and most of the species by their dried remains. They are still living things awaiting only another summer to build anew the parts above ground.

In the mowed prairies, late autumn shows a renewed growth of *Stipa spartea*, *Koeleria cristata*, and especially of *Poa pratensis* where these grasses occur. In addition a few other growing grasses and numerous rosettes, such as those of species of Antennaria, Solidago, Aster, Oenothera, and Gaura are to be found. With the coming of freezing weather, these still remain green, and if the soil is early covered with snow and the winter is not severe, some green leaves may endure throughout the winter. But life—dormant life—except for fruits and seeds, is found almost entirely within the protecting soil and scarcely at all above it.

In late winter and spring many mosses and numerous lichens are to be found on the damp soil between the tufts of sod. On low ground they are often very abundant, sometimes forming a more or less interrupted cover. When conditions are favorable they fruit abundantly. But their rôle is a very minor one in the prairies. It is only with the reappearance of young shoots from the awakening perennials that the beginning of a new season, a period filled with so many wonderful activities, is initiated. Again the prevernal aspect, soon to be followed by the vernal, is at hand.

HEIGHT-GROWTH AND PHYSIOLOGICAL ACTIVITY

Sociological periodicity depends upon the beginning, the duration, and the seasonal course of the struggle for existence. While phenomena such as flowering and fruiting are of great phenological importance, they may or may not coincide with the periods of maximum photosynthetic activity and consequent greatest demands for light, water, and nutrients. The growth of shoots, duration of foliage, fall of leaves, and development of new roots or replacement of old branches are physiologically quite as important. Such activities, so far as they have been determined, have already been discussed in dealing with the most important species; they will now be considered in their relations to the several aspect-groups.

A survey of the species characteristic of each aspect yields some important facts. All of the prevernal plants are of low stature, and carry on their life processes near the surface of the soil. Two (Draba and Androsace) are annuals or short-lived biennials. Some are short-lived as regards the parts above ground, e.g., Erythronium. None ever reach the midsummer

level of the grasses, but after a few weeks of activity in full light in spring, if they persist they are found only in the understory throughout the remainder of the year. Thus the period of anthesis is coincident with the period of maximum physiological activity of the prevernal species. For those that persist, the light factor becomes progressively more and more unfavorable. Moreover, no species of later aspects, save a few of the important grasses, make much growth during this period.

If certain sedges and the spike rushes of marshy grounds are omitted, approximately 70 per cent of the vernal species are likewise of low stature. These include Hypoxis, Fragaria, Viola, Oxalis, Galium, Astragalus, and others. A few, such as Senecio, have moderately tall flower stalks but these do not persist. Nearly all of those mentioned may be found in the understory throughout the growing season. A few are represented after midsummer only by scanty foliage and underground parts. Of the remaining 30 per cent, only a modicum, such as Zizia, Phlox, and Ceanothus, is conspicuous at or above the height of the dominants. Baptisia, Lithospermum, and Equisetum, representatives of species of larger stature in this aspect, are submerged by midsummer to the general level of the sea of grasses.

Thus the species characterizing the vernal aspect attain at this time not only their maximum flowering but also their maximum rate of growth and other physiological activity. The dominant grasses in the main have not yet so completely overshadowed them as to form a material handicap in the relation to light.[10] A few grasses, notably *Poa pratensis*, *Koeleria cristata*, and *Stipa spartea*, have grown very rapidly and likewise reached their period of flowering at the end or soon after the passing of this aspect. Likewise their maximum physiological activities for the year have been reached, and their life processes thereafter are on the decline. Only a few species such as Ceanothus and Zizia continue in their importance for any considerable time.

During the vernal aspect all of the estival and autumnal species have likewise started a vigorous development. The wave of prevernal activity has reached its crest and waned. The vernal species forge ahead in development of the ever increasing wave of estival and autumnal bloomers. The last, in general, reaches its crest of phenological and physiological activities latest. But week by week during the vernal period the struggle for light becomes more and more severe. Species of midsummer reach a moderate height in relation to the grasses; those of autumn continue to develop until they are mostly far above the dominants. Thus, species of the three major aspects—vernal, estival, and autumnal—all renew growth at about the same time. Since development is continuous until midsummer, the struggle is indeed severe. Then the decreasing demands for factors by maturing estival species

[10] There is much need for studies on the actual photosynthetic activity of the plants in the several layers of the prairie. Although some preliminary work has been done, these statements are based largely on photosynthetic activity as affecting growth above ground.

are compensated by the increasing demands of the still vigorously developing autumnal bloomers.

Plants of the estival aspect are strikingly of greater stature than those of either the prevernal or vernal ones. Although a very few species, such as Polygala, Specularia, Steironema, and Ruellia, are more or less hidden by the grasses, this class does not exceed about 11 per cent. About 39 per cent are approximately of the same height as the grasses and hence have a more or less equal relation to them as regards the light. Such species as Rosa, Rudbeckia, and Teucrium are representatives of this group. The remaining half of the estival bloomers, including Delphinium, several species of Asclepias, Petalostemon, Meibomia, and others, quite overtops the grasses and with *Psoralea floribunda, Baptisia leucantha,* and others, forms a distinct upper layer.

Among the autumnal bloomers none is found in the understory. Except Gentiana, all are conspicuous at or above the general level of the grasses. Indeed plants of the autumnal aspect are all of large size and many reach a height of 3 to 6 or more feet. Compared with the estival bloomers, as a group, they are considerably taller although they may not appear to be so because the lower parts are hidden by the tall grasses.

The several seasonal aspects are thus marked by species of varying stature. The prevernal and vernal are characterized by those of low or moderately low growth; the estival by plants of greater height, most of which have an equal advantage with the grasses in the competition for light. Autumnal species are nearly all characterized by large stature and are of sufficient height to reach the grass-level or indeed to extend several feet above it. In the prairie these adjustments to the light relation are very striking.

Only about 11 species are of much importance in the prevernal aspect. Nearly 40 have been tabulated as of major importance in the vernal one. Of estival bloomers there are about 70 that are of considerable importance. The autumnal aspect is characterized by about the same number of species (40) as the vernal one. Of the two leading families of forbs, the Papilionaceae contributes nothing to the prevernal aspect; 10 per cent to the vernal; 17 per cent to the estival; and 2 per cent to the autumnal. The percentages for the Compositae in the same sequence, however, are 18, 8, 17, and 88.

CONTACTS

The great prairie area under study gives way along the Missouri River to a belt of woodland varying in width from 2 to about 10 miles (Aikman, 1929). This is a northwestward portion of the deciduous forest formation which reaches to South Dakota. Extensions of woodland, which are postclimax, border the many tributaries of the Missouri in belts fringing the bluffs and sometimes extending somewhat over the adjacent hills. In south-

western Iowa and northwestern Missouri there occur some natural prairie groves. The extreme outposts of the forest are represented by relatively few species of trees and shrubs along the creeks and sheltered dry ravines which

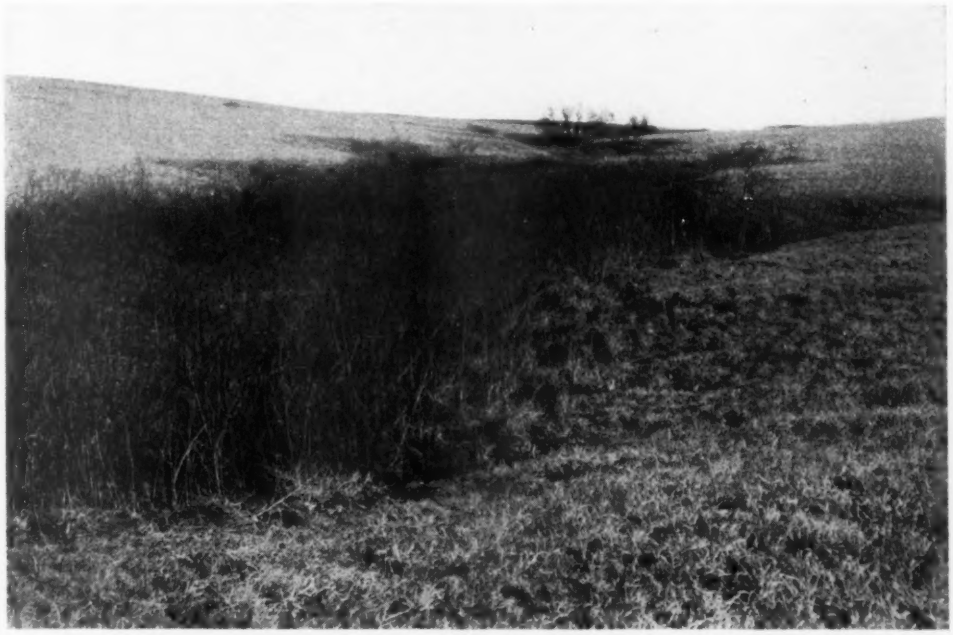

FIG. 113. *Rhus glabra* confined to ravines in drier portion of the prairie area; note also *Salix nigra* and *Acer negundo*, Lincoln, Nebr. Photo. in late winter.

FIG. 114. Invasion of *Rhus glabra* into low prairie. Unless mowed annually a thicket would result. Fairview, Kans., July 29.

more or less dissect especially the rolling portions of the prairie. Thus the grassland is in contact over a very great marginal area with the outposts of the forest (Fig. 112).

Along the forest border there is an ecotone where grass meets chaparral or woodland. This varies, depending upon the topography and its consequent effects upon the direct factors affecting vegetation, from a few feet on steep slopes to more than a mile on more uniform terrane. In such ecotones invasions are mutual, but this study is concerned only with the invaders of the grassland.

Two of the most characteristic shrubs that compete with the grasses are *Symphoricarpos vulgaris* Michx. and *Rhus glabra* L. (Fig. 113). The fruits of both species are widely distributed by birds. These shrubs renew growth early and develop rapidly and thus overtop the grasses. Both are well provided with excellent means of increasing their area vegetatively. Aside from underground stems, Symphoricarpos develops long runners which, however, take root with difficulty where the grass is dense. The branched underground stems of Rhus are often 20 or more feet in extent; by means of these its most effective invasion is accomplished (Fig. 114). Where either species becomes closely aggregated, the prairie vegetation disappears, the tolerant bluegrass being the last grass to succumb to the shade, if it does not remain as an understory. These shrubs often occur even in fairly dry soil, where they invade the little bluestem grasses. *Symphoricarpos occidentalis* Hook. plays a similar rôle but usually only on low ground.

Thickets of *Prunus americana* Marsh. extend far into the grassland. This tall shrub spreads widely by root offshoots; new stems arising 20 feet or more beyond the thicket border. Prairie grasses are replaced near the thicket by a marginal fringe of bluegrass; but under the dense shade and leaf mulch produced by the plum, it often entirely disappears.

Shrubby invaders in moist ground are *Salix interior* Rowlee, *Grossularia missouriensis* (Nutt.) Cov. & Britt., *Sambucus canadensis* L., and *Amorpha fragrans* Sweet. Frequently they develop dense clumps or thickets quite to the detriment of the grasses. But like all the preceding, in their struggle to make a home in the prairie they are greatly handicapped by the annual mowing.

Certain woody vines are not infrequently found in low prairies contiguous to woodland. Among these are species of Vitis, *Clematis virginiana* L., and *Celastrus scandens* L.

Cornus asperifolia Michx. and *Rubus occidentalis* L. extend outward from ravines; the former especially is a common shrub of forest margin. *Zanthoxylum americanum* Mill. is also sometimes found in mesic prairie borders.

In the better watered part of the area, especially in Iowa and Missouri, *Corylus americana* Walt. is a frequent invader. From protected north slopes

it may continue even over the crests of the hills and in spite of regular mowing occasionally occupy 15 to 50 per cent of the ground cover (Fig. 115). The new growth from established plants is developed so rapidly as to shade the grasses profoundly. Big bluestem is usually found around the bunches but only a light sprinkling of bluegrass within. In some areas Corylus also invades the little bluestem type.

While the fringe of marginal shrubs is usual, yet on steep slopes the boundary of the prairie is sometimes delimited directly by the shade of the overhanging branches of the trees rooted in the moist soil of the ravine. The chief species coming into such direct contact with the prairie are *Acer negundo* L., *Populus sargentii* Dode, *Ulmus americana* L., and species of Salix. Under such conditions the change is abrupt and there is no transition of bluegrass. But ordinarily a marginal zone at least several feet in width is maintained. Sometimes seedlings of *Ulmus americana* L., *U. fulva* Michx., *Tilia americana* L., and other trees are found well established on lower slopes quite apart from the forest border.

The ground oak (*Quercus prinoides* Willd.), with its top of many stems and extensive underground parts, was seen rarely and only on the eastern border of the area. But the bur oak (*Q. macrocarpa* Michx.) is a regular invader, working up ravines and thence out upon the uplands. Perhaps its most usual field of battle is in the big bluestem type bordering such areas, but it also frequently gains a foothold in little bluestem areas (Weaver and Kramer, 1932). When the main stem is cut it is replaced by sprouts and after repeated mowing a bush-like top is developed. This is often 2 or more feet high by midsummer and where moisture is sufficient for even a fair development the grasses all but disappear (Fig. 116).

The favorable conditions for growth along the forest margin are shown by the more luxuriant development of many prairie forbs. Certain woodland herbs also range into the prairie. Although the changes in the habitat from prairie to chaparral and woodland have been measured and the mechanism of invasion studied, the ecotone between prairie and woodland warrants further careful investigation (Weaver and Thiel, 1917; Pool, Weaver, and Jean, 1918). Over much of the area, however, it seems probable that chaparral and woodland could not extend their areas greatly even if unhandicapped by mowing and prairie fires (Clements, Weaver, and Hanson, 1929).

The chief contacts of the individual prairies at present, however, are those of ruderal and cultural areas such as the vegetation of roadsides, the crops and weeds of tilled fields and tame hay lands, and the pastured prairies that have so long been overgrazed that an almost new vegetation has developed. Such areas furnish abundant migrants for invasion.

Fig. 115. *Corylus americana* invading high prairie near Guthrie Center, Ia. *Quercus macrocarpa* in background on north-facing slope. Photo. July 23.

Fig. 116. Rolling prairie at Denison, Ia., with trees and shrubs in ravines and fringing woodland in pasture (upper right). *Ceanothus pubescens* in foreground.

INVASION AND SUCCESSION

Abandoned roads through the prairie, often consisting of a series of parallel tracks, show the invasion of ruderals in the subsere that was initiated by the disturbance. Here are also an abundance of native species which are otherwise sparse or subdominant. Characteristic species of the hard, compacted soil are *Polygonum aviculare* L., *Sporobolus neglectus* Nash, and *Verbena bracteosa* Michx. The bared central ridge and road margins may be populated by species of Lepidium, *Chenopodium album* L., *Hordeum pusillum* Nutt., *Bromus hordeaceus* L., *Boebera papposa* (Vent.) Rydb., and similar annuals.

Roads that have been abandoned a single year are often demarked to considerable distances in late summer and autumn by the dense growth of the now dry annual, *Aristida oligantha* Michx. In other places, especially where the prairie is extensive, species of sod-forming wheat grasses, otherwise rare except in the western part of the area, form a dense and almost continuous border. Or *Stipa spartea* Trin., because of its prolific seeding habit and burial of the fruits, may rather completely take possession. But neither the wheat grass nor any of the ruderals can successfully invade the prairie and indeed they gradually release their holdings. Stipa also diminishes in importance as the climax is reëstablished.

Succession has been observed on areas where the disturbance removed the surface soil to a depth of 4 to 6 inches, yet within 25 to 30 years the area had again developed the climax vegetation.

One of the chief disturbers of grassland is the pocket gopher (*Geomys bursarius* (Shaw) Rich.), a rodent of small size that thrives in fields of alfalfa and apparently has considerably increased its workings in the prairie since cultivation began 50 to 90 years ago. This burrowing animal brings to the surface the rich soil from the first foot and piles it in mounds 2 to 3 feet in diameter and 6 to 8 or more inches in depth. It pursues its tunneling throughout the growing season, cutting the roots of many species, especially of edible plants, and piling up the soil in such a manner as to bend down and cover even the tallest grasses. Sometimes these mounds are 4 feet in diameter and as many as 20 may occur in a square rod (Fig. 117).

Some of the species thus covered die, while others, such as the bluestems, come up through 6 to 8 inches of the loose soil the following spring. Often they push through only where the soil is shallower on the margins of the mounds. In such cases they may grow more luxuriantly and nearly twice as tall owing to the increased water supply. Hence the disturbed areas can be distinguished at a considerable distance. The less xeric big bluestem thus often replaces the little bluestem even where the latter is distinctly dominant, and various other species, such as *Elymus canadensis* and *Panicum virgatum*, may gain a foothold in the sod. Certain species typical of the prairie, such

as *Agrostis hyemalis* and *Stipa spartea*, as well as many ruderals, as *Aristida oligantha* and mat-forming species of Euphorbia, mark the short sere before the bluestems again regain possession. Where the prairie is disturbed over

FIG. 117. Prairie in spring showing characteristic disturbance due to pocket gophers.

FIG. 118. Flood plain of the Platte River near Fremont, Nebr., July 15. In such areas various stages in the development toward climax prairie are found.

a greater area as by stacks of hay, a longer but somewhat similar sere is initiated.

Invaders from ruderal areas and cultivated fields are indeed few and, with rare exception, of no importance unless some disturbance has occurred which has handicapped the development of the natural vegetation or broken the cover of the soil. A few ruderals, notably the short-lived *Tragopogon pratensis* L., invade the prairie even where undisturbed but after a year or more of some local abundance they entirely disappear.

The most persistent and successful invader since the settlement of the country and the cessation of prairie fires is the Kentucky bluegrass. Not only is it found in nearly all of the prairies of the whole region but also it extends from lowlands to high ground. It is much harmed by fire but can tolerate considerable shade. Its early growth in mowed grassland is notable. Under natural competition with the undisturbed prairie it can merely survive. When the prairie is grazed, it increases rapidly in abundance at the expense of the other species and thousands of areas of native grassland have deteriorated into bluegrass pastures. All degrees of retrogression may be found.

Where low prairies are mowed too often, disturbed by occasional flooding, pastured in late fall or early spring, or where the cover is broken in the process of "hay making," invasion by timothy (*Phleum pratense* L.), red clover (*Trifolium pratense* L.), or white sweet clover (*Melilotus alba* Desv.) is likely to occur. In fact, the primary cause for the breaking of many areas of prairie in Iowa and Missouri was the serious invasion by one or more of these species. Sweet clover is a coarse biennial with much food stored in a fleshy taproot. Like bluegrass it makes an early growth, often several stems arising from a single root. It far overtops the grasses, and seeds prolifically. The coarse stems become woody by the end of summer and where the plants are abundant they greatly depreciate the value of the much prized prairie hay. Many farmers retain their low prairies against its invasion by cutting the sweet clover plants early in June.

In the wetter portions of the greater valleys especially, but also over the region generally, wet areas of greater or lesser extent occur. Here are found various stages of the hydrosere illustrating the transition from wet areas to prairie. The development from reed swamp, dominated by *Scirpus validus* Vahl, *Typha latifolia* L., *Sparganium eurycarpum* Engelm., and *Phragmites communis* Trin., to big bluestem prairie was quite clearly demarked.

A halfway point in the development is characterized by the *Spartina michauxiana* consocies, including *Tripsacum dactyloides*. On slightly drier soil this gives way to the *Panicum virgatum-Elymus canadensis* type in the transition to the bluestem prairie. The latter has been included in the term

low prairie. Numerous dominants of sedge meadow and relict stands of plants from the reed swamp are found in still wetter areas. These may occur either as extensive pure stands where the habitat is continuously uniform, or, more often, they form alternes of greater or less extent. Chief among them are *Persicaria muhlenbergii* S. Wats., *Carex vulpinoidea* Michx., *Leersia oryzoides* Poll., mixed communities of various sedges and rushes, *Eleocharis palustris* (L.) R. & S., *Scirpus atrovirens* Muhl., and *Phalaris arundinacea* L.

Sometimes the transitions are sharp and the associes or consocies well defined. Frequently two or more occur in various mictia, alternate repeatedly over large areas, or give way gradually one to the other. While areas dominated and indeed almost completely covered with stands of *Persicaria muhlenbergii* are common, this tall, erect, perennial forb is more often a component of the other communities. Very extensive, dense, and nearly pure communities of *Carex vulpinoidea* (except for coarse forbs) cover large areas and recur again and again. Areas and alternes of *Leersia oryzoides* are also common but they are not so numerous as the preceding. Where they are found the vegetation is likewise tall and dense. This grass is also found abundantly as an understory in late stages of the development of the reed swamp.

Carex festucacea Schkuhr. sometimes covers extensive areas with a dense growth as does also *C. hystricina* Muhl. Much more usually, however, mixed stands including *Juncus torreyi* Coville, *Scirpus fluviatilis* (Torr.) A. Gray, *Fimbristylis interior* Britton, and various others occur in extensive mixtures.

Eleocharis palustris is the most important of the spike rushes. Areas occupied by it, whether small or large, are clearly delimited by their dark green color. This species forms an exclusive sod. The terete, leafless stems, crowned in late spring with terminal cones, are densely aggregated. The spike rushes, like various sedges, occur more or less regularly as an understory not only in many communities of the wet meadow but also in slough grass and sometimes in small numbers even in the wettest areas occupied by big bluestem.

The tall coarse *Scirpus atrovirens* is also perennial with slender rootstocks but the coarser and triangular culms form a more open growth. The dark green, leafy plants commonly reach a height of 3 to 4.5 feet. When the species is in fruit, the almost pure growth appears very distinctive, the black umbels of spikelets characterizing it from afar. It approaches the species of reed swamp in its water relations. *Phalaris arundinacea* forms clearly defined local communities usually of no great extent. The sod is dense and the plants are 3 to 5 feet tall.

As the habitat warrants many of the plants intermingle more or less with Spartina especially in its early possession of wet land. Hundreds of acres

of "first bottom" lands along the Missouri and Platte Rivers and their tributaries are clothed with wet meadows where tall panic grass and nodding wild rye form great alternes with slough grass, *Carex vulpinoidea*, and various combinations of sedges. Often these more or less equally share such areas (Fig. 118).

Where Spartina or Tripsacum is best developed there are few or none of the coarse herbs common to low ground. Only a few remnants of sedges, rushes, bluegrass, and other species occur in the understory, so dense is the shade. This is also true for dense growths of *Carex vulpinoidea* and *Scirpus atrovirens*. But where the stands are more open and especially where mixtures abound, forbs are abundant. Most of these are common to the several stages in development although they may vary greatly in abundance and stature. Some disappear before the well drained soil of the big bluestem consociation is attained. This grassland community then acquires new species from the upland, which here reach their mesic limit. A few are characteristic of very wet soil only.

In open stands of Spartina, a low layer of *Oxalis violacea*, *Fragaria virginiana*, *Viola papilionacea*, and *V. palmata* often occurs. A higher one consisting of *Galium tinctorium*, *Steironema ciliatum*, *Anemone canadensis*, and *Equisetum arvense* is also common. Similar layers are more or less developed under open stands of *Carex vulpinoidea*, and mixtures of carices and certain of these species are found even in wetter habitats. Almost throughout the sere *Lythrum alatum*, *Pycnanthemum flexuosum*, *Vernonia fasciculata*, *Teucrium canadense*, *Bidens frondosa*, and others compete with the sedges for a place in the sun. Many water-loving grasses occur, such as *Beckmannia erucaeformis*, *Cinna arundinacea*, *Elymus jejunus*, and *Panicularia nervata*. Such areas, moreover, present a very uneven appearance because of an abundance of such tall coarse forbs as *Helianthus grosseserratus*, *H. maximiliani*, *Asclepias incarnata*, *A. sullivantii*, *Aster salicifolius*, *Meibomia illinoensis*, *Cicuta maculata*, *Verbena hastata*, and *Heliopsis scabra*. Areas of Eleocharis, however, are nearly always relatively free from forbs.

In still wetter areas such species as *Mentha piperita* L., *Rorippa sinuata* (Nutt.) Hitchc., *R. palustris* (L.) Besser, *Iris versicolor* L., and *Lippia lanceolata* Michx. are found. In regard to the sequence of succession no further details need be given. In fact this outline merely constitutes a basis for further study.

Where wet or moist ravines occur many species of low wet lands extend as narrow belts of vegetation far into the uplands. Thus one or several of the various plant communities just described may be encountered in passing from one hillside to the next. Farther up the ravine, tall, coarse forbs mark the course of the depression and indicate by their increased or decreased stature the supply of run-in water (Fig. 119).

Numerous, small local areas of soil more or less impregnated with alkali occur throughout the drier parts of the region. The salts are in the main white alkali and in the extensive areas along Salt Creek practically pure

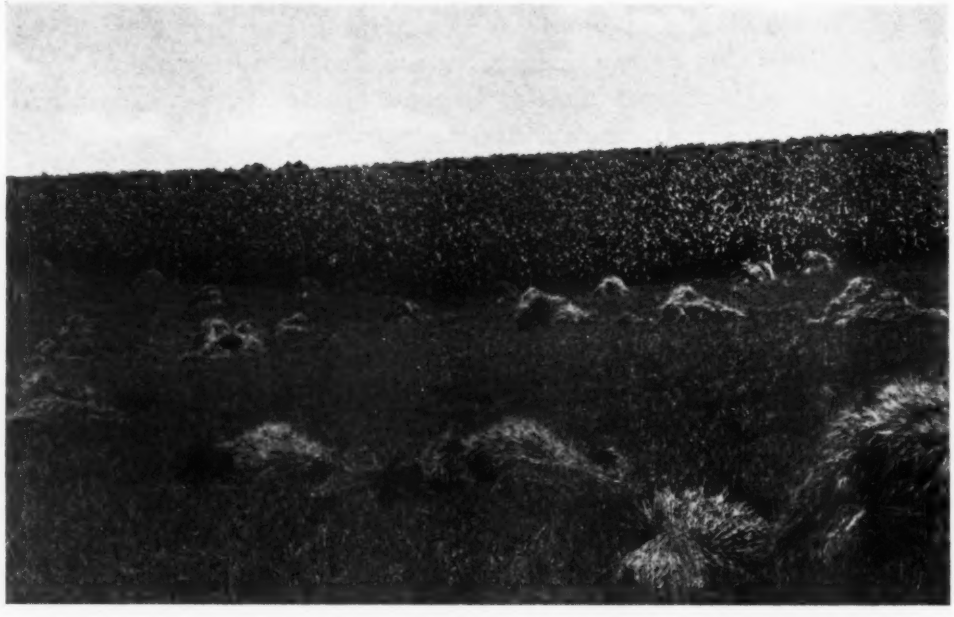

Fig. 119. Ravine in big bluestem prairie demarked by *Solidago altissima, Helianthus grosseserratus,* and other coarse forbs.

Fig. 120. Successors of the prairie: fields of wheat and maize. The native grasses are rapidly disappearing before the breaking plow and as a result of close grazing.

sodium chloride. Where they exceed 2.5 per cent in concentration few or no plants occur. The most tolerant species is *Salicornia rubra* A. Nelson which endures at least 2.3 per cent of salt. Zones of nearly pure growths of *Suaeda depressa* (Pursh) S. Wats., *Atriplex hastata* L., and *A. argentea* Nutt., followed by salt grass, *Distichlis spicata* (L.) Greene, are to be found where the depression is of considerable extent and the surface slopes gradually to higher land. Distichlis gradually gives way to more or less nearly pure growths of species of Agropyron and these in turn to typical climax prairie (cf. Schaffner, 1898).

The early stages of the halosere are characterized by a nearly pure growth of relatively few species and rather sharp ecotones between consocies. The salt-grass and wheat-grass communities are most abundant over the area as a whole. *Distichlis spicata* is a sod former and usually occurs in dense, almost pure stands, the density and continuity of the sod indicating in general the degree of salinity and condition of water supply as well as the degree to which the soil is more or less favorable to its development. The soil is frequently of high clay content, subject to cracking during drought, and of poor granulation.

Pure stands of wheat grass, chiefly *Agropyron pseudorepens* Scribn. & Smith and *A. smithii* Rydb., cover large areas. Where the salt grass is still present as an understory the wheat grass forms an open stand and the plants are usually dwarfed. Where the sod is pure and of moderate density 500 flower stalks may occur to the square meter. On wet years and in the best developed stands they are much thicker.

Certain other grasses frequent alkali flats. *Sporobolus airoides* Torr. is often found associated with Distichlis or in the ecotone between this and the wheat grass consocies. *Sporobolus heterolepis* A. Gray is locally often very abundant among the wheat grasses. *S. asper* (Michx.) Kunth occurs frequently and abundantly as does also *S. cryptandrus* (Torr.) A. Gray, westward. *Poa compressa* L., and certain other species of Poa may occur in pure or nearly pure growths, as do also alternes of *Juncus tenuis* Willd. *Eragrostis pectinacea* (Michx.) Steud. frequently becomes densely aggregated. *Eleocharis acicularis* (L.) R. & S. may make a good growth under the wheat grass in early summer. *Hordeum jubatum* L. is a weedy annual that is frequently found widely distributed as is also *Polygonum ramosissimum* Michx. Alternes of *Bulbilis dactyloides* (Nutt.) Raf. and *Bouteloua gracilis* (H. B. K.) Lag. are not infrequent on these hard, compact soils and are nearly always accompanied by such characteristic species as *Hedeoma hispida* Pursh, and *Festuca octoflora* Walt. Sometimes the short grasses form a lower story under the wheat grass. Competition of other tall grasses is removed because of the unfavorable habitat.

Just as few forbs are found in communities of salt grass, so too the

wheat-grass sod is often nearly free of them. Certain species, however, are not only characteristic but also sometimes fairly abundant. Chief among these are *Asclepias verticillata* L., *Aster multiflorus* Ait., *Iva ciliata* Willd., and *Artemisia gnaphalodes* Nutt., although several other species from the adjacent prairies are common. Nearly always the forbs indicate by dwarfness of stature the severe conditions of life.

The ecotone between the Agropyron community and the low prairie is frequently characterized by an increase in *Sporobolus asper* and *Panicum virgatum*. If sufficient moisture is present for the growth of *Spartina michauxiana*, this species is dwarfed in stature and of open growth since it is intolerant of alkali. The first occurrence of *Andropogon furcatus* and *Sorghastrum nutans* is usually as large clumps or bunches, but soon these give way to the characteristic open sod of low prairie.

SUMMARY

1. One hundred thirty-five selected areas of tall-grass prairie were studied during a period of five years. They were representative of the vegetation of the eastern one-third of Nebraska, the western one-third of Iowa, and adjacent areas in Kansas, Missouri, South Dakota, and Minnesota. They varied in size from 20 to 360 acres and were rather uniformly distributed throughout an area of 60,000 square miles.

2. The study was made to determine the structure, development, and continuity of the prairie; to better understand the importance, significance, and utilization of grassland; and to furnish a permanent record of a rapidly vanishing vegetation.

3. The topography includes long lines of loess bluffs, great areas of nearly level lands, extensive tracts of rolling hills with well drained valleys, and broad flood plains. The whole area has been glaciated, except the loess plains on the western border.

4. Mature soils have dark colored A horizons with granular structure and yellowish or brownish B horizons with columnar structure. They are relatively non-acid, unleached, well aerated, rich in organic matter and mineral nutrients, and have great depths. A lime layer occurs in the subsoil at a depth of 5 to 8 feet in the western part of the area.

5. Moderately long cold winters are followed by hot summers with average day temperatures between 75° F. and 85° F. The growing season (April to October) is characterized by much sunshine, considerable wind, an average daily evaporation of 20 to 30 c.c., and an average day relative humidity between 40 and 80 per cent.

6. Mean annual precipitation varies from 25 inches in the northwest to 36 inches in the southeast. About 78 per cent falls in fairly well distributed showers during the growing season.

7. Water content of soil varies widely and rapidly in the surface 6 inches, but is rarely reduced to the hygroscopic coefficient. Water is practically always available for growth in the second 6-inch level. At greater depths the available supply usually ranges between 5 and 25 per cent, and the deeper subsoil is constantly moist.

8. The prairie is a community of great complexity. Variations in its structure result from differences in regional precipitation, local differences in habitat factors, and from changes brought about by the advance of the seasons.

9. All of the dominant and nearly all of the subdominant species are perennials. Climax prairie is a closed community; the water content and light are so fully utilized that few seedlings of native species ecize and invaders are excluded. Reproduction is largely vegetative.

10. The struggle for water has resulted in the development of deeply penetrating and usually widely branching root systems. These are segregated into several absorbing levels, constituting one of the chief adaptations of the plants to their environment.

11. Competition for light has resulted in layering. Certain forbs always remain near the surface of the soil; some with long, erect stems are leafy only above the grasses; others produce much foliage from soil surface to leafy top, often reaching a greater height than the grasses. The effect of the community upon the individual is pronounced.

12. The plants develop rapidly; even autumnal forbs begin vigorous development in early spring, and the dominant grasses complete their vegetative growth in July. Hence the species may be identified throughout the summer by their vegetative characteristics.

13. Investigations in each prairie dealt with the types of grassland, the transitions from one to the other, percentage composition in terms of the dominant grasses and forbs, basal cover, and structure of the foliage cover.

14. Six types of grassland occur, two of which are subclimax. Those of greatest importance are dominated by *Andropogon scoparius* and *A. furcatus*, respectively. Together they constitute fully 80 per cent of this grassland.

15. The *Andropogon furcatus* consociation occurs on moist slopes and well aerated lowlands. Big bluestem is dominant because of its rapid development, dense, sod-forming habit of growth, great height (5 to 10 feet), long life, and tolerance of its seedlings to shade.

16. The *Spartina michauxiana* consocies occupies extensive areas of wet, poorly aerated soils. Slough grass is dominant because of its growth to a height of 6 to 10 feet in dense, pure stands. The basal cover is only 1 to 3 per cent, yet shade is so dense as to exclude other grasses.

17. The *Panicum virgatum-Elymus canadensis* consocies is an intermediate lowland type of much less extent. Tall panic grass is a coarse,

sod-forming species, rarely found in extensive pure stands, furnishing a basal cover of only 2 to 5 per cent. Nodding wild rye is a coarse grass, 3.5 to 4.5 feet tall, that occurs in small bunches.

18. The *Andropogon scoparius* consociation is the most extensive upland type and probably exceeds in area all of the other grassland types combined. Little bluestem is dominant because of its vigorous development, tillering early and abundantly, and its fine, deep, extremely well branched root system.

19. The *Stipa spartea* consociation covers extensive areas on dry ridges and slopes in the central and northern parts, occurring mostly as broad alternes with *Andropogon scoparius.* Needle grass forms small, widely spaced bunches, renews growth early, attains a height of 3 to 4.5 feet, and blossoms in June.

20. The *Sporobolus heterolepis* consociation is a minor upland type of dry soils. Prairie dropseed forms large bunches, often occurs in nearly pure stands, reaches a height of 1.5 to 3 feet, and has a basal cover of 8 to 15 per cent. Its chief contacts are with little bluestem and needle grass with which it often mingles.

21. Distribution of the major grasses in the Andropogon types was uniform throughout the area. Hill crests and drier slopes were dominated by *A. scoparius* which furnished 40 to 90 per cent of the basal cover. On moist midslopes dominance was often shared equally by the bluestems. On lower slopes and in ravines *A. furcatus* dominated and on well drained lowlands furnished 85 to 98 per cent of the cover.

22. *Andropogon furcatus, Poa pratensis, Stipa spartea,* and *Sporobolus heterolepis* were chief accompanying species on uplands and *Poa pratensis, Sorghastrum nutans,* and *Panicum virgatum* on lowlands.

23. *Stipa spartea* constituted 35 to 80 per cent of the basal cover in its consociation; important grasses were *Andropogon scoparius, A. furcatus, Poa pratensis,* and *Sporobolus heterolepis.*

24. The average basal cover in the *Andropogon scoparius* type was 15.3 per cent, varying but little from year to year. *A. scoparius* furnished 55 per cent, *A. furcatus* 24.8 per cent, *Poa pratensis* 4.7 per cent, and forbs 4.1 per cent. Foliage cover varied from 55 to 100 per cent.

25. Basal cover increased 5 per cent in the wetter area (precipitation 32 to 36 inches) over that of the drier one (25 to 32 inches). *Andropogon scoparius* and other xeric grasses decreased but *A. furcatus* and other mesic grasses increased in abundance.

26. The average basal cover in the *Andropogon furcatus* type was 13.3 per cent; *A. furcatus* furnished 78 per cent, *A. scoparius* 2, *Poa pratensis* 8.8, and forbs 3.6. The foliage cover was usually 90 to 100 per cent.

27. Basal cover increased 9 per cent in the wetter area over that of the

drier one. The bluestems showed little change but several xeric grasses decreased in abundance.

28. The average basal cover in the *Stipa spartea* consociation was 10.9 per cent. *Stipa spartea* furnished 51 per cent, *Andropogon scoparius* 17.7, *A. furcatus* 17.5, *Poa pratensis* 5.1, and forbs 2.4.

29. *Sporobolus heterolepis* often formed 60 to 65 per cent of the basal cover in its consociation. Other important grasses were *Andropogon furcatus, A. scoparius,* and *Poa pratensis.*

30. The foliage of *Andropogon scoparius* averaged 5 to 9 inches higher in the southeast than in the drier southwest or northwest. That of *A. furcatus* showed differences of 6 to 12 inches.

31. Bunches of *Andropogon scoparius* and other grasses were more completely filled with stems southeastward. Flower stalks were larger and more abundant, occurring even during dry years; yields of hay were greater.

32. Of 25 minor grasses and sedges of uplands the most important are *Poa pratensis, Panicum scribnerianum, P. wilcoxianum, Sporobolus asper,* and *Carex pennsylvanica. Poa pratensis* has spread widely since the cessation of prairie fires and under the practice of annual mowing.

33. *Poa pratensis, Agrostis palustris, Carex vulpinoidea, Tripsacum dactyloides,* and *Eleocharis palustris* are the most important of 22 minor grasses, sedges, and rushes characteristic of wetter grasslands.

34. The 75 most important forbs of uplands were grouped into 5 classes according to their abundance, size, duration, density, gregariousness, and effect upon the cover of grasses. They were then arranged in the order of their importance as indicated by their percentage occurrence in societies of the first and second class.

35. *Amorpha canescens,* a half-shrub behaving as an herb under annual mowing, is the most important. It was found in all but 7 per cent of uplands and ranked as a society of the first class in 74 per cent. This shade enduring legume is leafy to the base of the stems which attain a height of 1.5 to 3 feet. The widely spreading roots absorb to depths of 6 to 16 feet.

36. *Helianthus rigidus, Aster multiflorus, Antennaria campestris, Erigeron ramosus, Solidago glaberrima,* and *Psoralea argophylla* are important species. All occurred in at least three-fourths of the uplands and ranked as societies of the first class in one-third or more.

37. The 67 most important forbs of lowland prairies were classified in the same manner as the upland forbs.

38. *Galium tinctorium,* a densely aggregated perennial with erect stems, is the most important. Attaining a height of 8 to 18 inches, this very tolerant species forms a dense understory in wet grasslands and in many big bluestem prairies. It occurred in 74 per cent of the lowlands and ranked as a society of first or second class in 52 per cent.

39. *Fragaria virginiana, Steironema ciliatum, Aster salicifolius, Anemone canadensis, Solidago altissima,* and *Silphium laciniatum* are important species. All occurred in at least two-thirds of the low prairies, and ranked as societies of the first or second class in 40 per cent or more.

40. Compositae furnished 34 per cent of the leading forbs of the entire area; the Papilionaceae contributed 13 per cent; the Asclepiadaceae and Labiatae 5 and 4 per cent, respectively.

41. Over 200 additional species occurred only in less than 10 per cent of the prairies.

42. The prevernal aspect begins in March and closes late in April. Only 11 species are important. The plants are of low stature and occur near the soil surface. Anthesis is synchronous with maximum physiological activity.

43. The vernal aspect begins late in April and continues until late in May, initiating rapid vegetative growth of plants of summer and autumn. Forty species are important in this aspect. About 70 per cent are of low stature. Only a few are conspicuous after midsummer at or above the level of the grasses. Maximum physiological activity of vernal species occurs during the aspect.

44. The estival aspect is initiated late in May by the blossoming of *Stipa spartea, Koeleria cristata,* and many forbs. Dominant grasses of uplands are 6 to 8 inches tall, those of lowlands 12 to 18 inches. Seventy species of forbs are of importance. About 39 per cent are nearly the same height as the grasses; 11 per cent are found in the understory; and 50 per cent form a layer above the grasses.

45. The autumnal aspect begins late in July. The grasses have passed from a stage of active development to one of approaching fruition and maturity. The aspect is characterized by the blooming of 40 important species of forbs, 88 per cent being Compositae. All extend above the grasses, many reaching a height of 3 to 10 feet.

46. Greater height of species of lowlands has probably resulted from a greater water supply and especially from the struggle for light.

47. The hiemal aspect follows the gradual deterioration and death of the plant parts above ground, which is hastened by repeated frosts. Life, except in seeds, is found almost entirely within the protecting soil.

48. Contacts of the prairie are with deciduous forest along the Missouri River and postclimax woodland along streams. *Corylus americana* and other shrubs often form an ecotone; thickets of Symphoricarpos, *Prunus americana,* and *Rhus glabra* occur in the prairie. Chief contacts are with cultivated fields and pastures.

49. Invasion occurs along roads through prairie; the subsere is dominated for a short time by ruderals. Rodents cause disturbance and initiate subseres. Invaders into stabilized prairie, except *Poa pratensis,* are few and

transient. Local disturbance may permit invasion of *Phleum pratense, Trifolium pratense,* or *Melilotus alba.*

50. Communities succeeding the reed swamp stage are dominated respectively by *Persicaria muhlenbergii, Carex vulpinoidea, Leersia oryzoides, Eleocharis palustris,* and *Phalaris arundinacea.* These are replaced by *Spartina michauxiana.*

51. Succession in alkali soil begins with *Salicornia rubra* and terminates in low prairie.

52. The prairie is rapidly disappearing as a result of breaking and grazing.

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Sworn to and subscribed before me this 5th day of March, 1934.

C. B. MARKHAM,
Notary Public.

My commission expires August 7, 1934.